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# Annals

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# Annals of the Missouri Botanical Garden

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## A COMPARATIVE STUDY OF CONIDIAL FORMATION IN CEPHALOSPORIUM AND SOME RELATED HYPHOMYCETES<sup>1</sup>

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### I. INTRODUCTION

Among the organisms isolated by the author from dermatomycoses at the Barnard Free Skin and Cancer Hospital, St. Louis, Missouri, a red yeast, identified as *Torulopsis mucilagiosa*, appeared frequently. On ordinary media it formed a rose-red, pasty, and superficial colony; in liquid, a basal deposit and some pseudomycelial proliferation throughout the solution. Upon nitrate agar of Stellung-Dekker ('31) the growth was homogenous and scanty on the surface and cloudy-white within the medium. Microscopic examination revealed a pseudomycelium bearing numerous lateral spore balls reminiscent of *Cephalosporium* (pl. 2, fig. 43). This suggested a further study of the cause of the deviation and the relationship of the budding and cephalosporial states. A cursory investigation of the pertinent literature disclosed much confusion regarding the types of Hyphomycetes which form cephalosporia (spore balls). Hence, the problem has been extended to a comparative morphological study involving principally

<sup>1</sup> An investigation carried out in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

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forms which may grow parasitically or saprophytically upon the human skin.

It is the primary aim of this dissertation to explain the mechanism of cephalosporial production and to correlate such findings with data on other types of spore-producing organs. Observations of the pathogenicity of these organisms for man are recorded. Also, on the basis of methods of production and kinds of spores, as well as upon other physiological and morphological observations, the group is discussed systematically. Present treatments are criticized and emended, at least in consideration of the few forms studied.

## II. MATERIALS AND METHODS

Investigations have been made upon the following species. For further discussion of systematics see p. 37.

ORGANISM	PLACE OBTAINED
<i>Allescheria Boydii</i> Shear	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium kiliense</i> (Gruetz) Hartmann	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium niveolanosum</i> Benedek	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium rubrobrunneum</i> Nannizzi	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium Serrae</i> Maffei	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium Stuehmerti</i> Schmidt & Beyma	Centraalbureau voor Schimmelcultures, Baarn
<i>Cephalosporium symbioticum</i> Pinkerton	Barnard Free Skin and Cancer Hospital, St. Louis
<i>Clonostachys Araucaria</i> Corda	Centraalbureau voor Schimmelcultures, Baarn
<i>Clonostachys Araucaria</i> var. <i>rosea</i> Preuss	Centraalbureau voor Schimmelcultures, Baarn
<i>Clonostachys Araucaria</i> var. <i>confusa</i> Pinkerton	C. Thom
<i>Clonostachys spectabilis</i> (Harz) Oudem. & Sacc.	Centraalbureau voor Schimmelcultures, Baarn
<i>Gliocladium deliquescens</i> Sopp	C. Thom
<i>Gliocladium fimbriatum</i> Gilman & Abbott	C. Thom
<i>Gliocladium penicilloides</i> Corda	C. Thom
<i>Gliocladium Vermoeseni</i> (Biourge) Thom	C. Thom
<i>Scopulariopsis brevicaulis</i> (Sacc.) Bainier	C. Thom
<i>Torulopsis mucilaginousa</i> (Jørgensen) Ciferri & Redaelli	Barnard Free Skin and Cancer Hospital, St. Louis

The stock medium was glycerine agar (nutrient agar plus 6 per cent glycerine, pH 6.9). The following agars were also used: maltose (pH 5.4), Sabouraud's dextrose (pH 5.6), wort (pH 4.8), Raulin's (pH 4.15), Czapek's (pH 4.43), Richards' (pH 4.36), Endo's (pH 7.52), Gorodkova-Maneval modified (pH 6.8), nitrate (pH 5.5), nutrient (pH 6.0), corn meal (pH 6.0), potato dextrose (pH 5.7); these liquids—nutrient (pH 6.0), lactose (pH 6.8), litmus milk; also sterilized carrot plugs, gypsum blocks, Bacto-beef blood serum (pH 7.3), and glycerine agar double strength plus 50 per cent Bacto-blood (pH 6.0). The latter gave the most luxuriant and rapid growth.

Cultures were made chiefly in test-tubes and bits of them were examined at intervals in semi-permanent mounts of Amann's ('96) lacto-phenol plus a 1 per cent aqueous solution of anilin blue. Such served for gross morphology and even showed a fair degree of the more minute structure of the phialide. The proper relationships of the various parts of the organism and their comparative colonial characteristics are shown in the photographs of Petri plate cultures containing Czapek's agar (pl. 6). Cultures were also examined directly under high power after placing a cover slip over a sparsely grown section of the agar. Camera-lucida sketches were made of relevant structures and photomicrographs were taken where possible, but due to the minuteness of the conidial fructifications the latter procedure was not very practical.

Hanging drop and agar preparations made in van Tieghem cells were of little use, since the fruiting bodies were produced pendant in the air and hence not discernible under oil. Agar slide cultures, produced by placing a few drops of warm agar upon a sterile slide, inoculating, and applying an aseptic cover slip (No. 1, 24 × 40) when the agar was cool enough to barely spread, were found to be most helpful, giving a comparatively small circular agar matrix from which aerial fructifications radiated. The narrow ends of the cover slip were sealed with paraffin to make the mount rigid, and the microcultures incubated at room temperatures in sterile staining jars with moist filter-paper at the bottom. On the second day the formation of spores could sometimes be observed under oil immersion.

Material for cytological study was grown on Raulin's agar and on glycerine agar. Hermann's fluid<sup>1</sup> was employed for killing and Jeffrey's celloidin technique was followed for the earlier work. The fixing agent was applied directly to the slant culture which was evacuated for about fifteen minutes to remove air from the agar containing submerged growth. After twelve hours the material was washed for an equal time in slowly running water, following which the agar was cut into small blocks about 5 mm. square and run through the alcohols.

Since it was impossible to get celloidin sections thinner than 10  $\mu$ , for studying structures of 2  $\mu$  average diameter the paraffin method was tried. After the agar culture had been cut into small bits, good infiltration was secured and sections were obtained 1, 3, 5, 8, and 10  $\mu$  in thickness. The very thin ribbons had the disadvantage that so few aerial phialides were encountered in a slice. Nevertheless, nuclear orientation was clearer in the paraffin material, whereas accessory cytoplasmic inclusions and external mucoid structure were more noticeable in the celloidin matrix. Haidenhain's iron-alum haematoxylin was used exclusively for staining, applied according to the following schedule: hydration, one hour in 20 per cent USP hydrogen peroxide, washing, 4 per cent iron alum two hours,  $\frac{1}{2}$  per cent haematoxylin twelve hours, slight destaining with 2 per cent iron-alum while watching through the microscope, dehydration, clearing in xylol, and mounting in Canada balsam. The species cytologically investigated include: *Allescheria Boydii*, *Clonostachys Araucaria*, *C. Araucaria confusa*, *Cephalosporium Serrae*, *Gliocladium deliquescens*, and *G. penicilloides*.

An attempt was made to compare the wall composition of the ordinary mycelium and of the phialide by use of the polarizing microscope. The thinness of the cell walls and the difficulty of obtaining sufficient light with the higher magnifications prevented satisfactory observation. Hanging drop cultures, where the fructifications could be brought into focus, served best.

<sup>1</sup> The formula is: platinic chloride 3 cc. in 12 cc. of distilled water; osmic acid 2 cc.; glacial acetic acid 1 cc. A fresh solution should be used for each application.

All of the organisms were grown at 30° C. The cultures were usually incubated in the light, since darkness often caused loss of color without other apparent changes. In an attempt to induce the perfect stage, glycerine agar was employed with H-ion concentrations from 3.8 to 7.6; and the following special media were utilized: gypsum blocks, Gorodkova-Maneval medium, carrot plugs, and corn meal agar. Attempts at cross fertilization were made, and while no perfect states were induced some interesting subsidiary observations were obtained.

### III. THE CONIDIAL APPARATUS

#### A. THE CONIDIOPHORE

The forms here investigated are believed to be closely related to *Penicillium* of the sub-family Aspergilleae in the Hyphomycetes. The form-genus finds its perfect stage in *Carpenteles* Langeron ('22) of the ascomycetous order Plectascales, although the latter name is by no means in common usage. Its conidial apparatus consists of a basal stalk cell from which branches arise variously but more or less regularly for each species. The end cell of the penicillus, called the phialide, cuts off spores terminally in chains. The spores are temporarily adherent, due to connectives which later become disjunctors and probably are formed from the old wall of the phialide. In the material of the present study there are no disjunctors, and the spores mutually adhere in a more or less globular mucilaginous mass around the phialide. The spore ball is termed the cephalosporium in contrast to the entire fructification, or cephalophore. In most cases the cephalosporia are characteristic of the aerial mycelia, although submerged ones have been noted in *Cephalosporium Serrae*. The complete conidiophore varies from a short branch no longer than the spores produced (e. g. *Allescheria Boydii*) to a complex structure equivalent to the penicillus (e. g. *Gliocladium*); but in all cases where cephalosporia are produced the mechanism seems identical.

#### 1. HISTORICAL

a. *On conidial production in the Aspergilleae and related forms.*—Brefeld ('74) was one of the earliest to observe criti-

cally conidiophore formation although his methods were necessarily crude. He saw no need for the assumption of a special membrane outside that of the conidium, and thought that the process was one of budding. Referring to the forms with disjunctors, Seynes ('86) stated that the phialide wall formed the connective and the conidia differentiated their own walls within. The following statement of de Bary's ('84) exhibited keen insight although his interpretation was incorrect:

Bei reichlich inner halb enger und mit enger Mündung versehener Behälter abgeschnürten Sporen wird durch die Gallert- oder Gummiabscheidung die Entleerung aus dem Behälter bewirkt, indem die durch Wasseraufnahme quellende Masse aus der Mündung hervortritt. [p. 75].

He believed that there was a gelatinous substance around the spore (a product of its outer lamella) which became deliquescent by addition of moisture and so caused coherence.

A number of investigators attempted to interpret the method of spore production in *Thielavia basicola* of the Plectascales, following Zopf's original description in 1890. He reported an acropetal succession of spores whose lateral walls were differentiated into two layers, the outer being a sheath through which the conidia emerged successively due to the swelling of the mucilaginous middle lamella upon the addition of water. Gilbert ('09) thought that endoconidia were formed in the phialides and emitted consecutively by the force of the growing protoplasm in the basal part of the cell. Brierley ('15) was the first to make a definite attempt to determine the method of conidium production, and he concluded that the method previously called endoconidial was in reality merely acrogenous, being peculiar only in the mechanism of liberation. The conidium put down an additional wall within the parental one which was then ruptured and the new spores were constantly formed from below. The illustrations of the mode of new wall differentiation are quite anomalous. It was Duggar's view ('09) that the endoconidia were ejected by osmotic pressure. Guegen ('05) cited *Gliomastix chartarum* as an example of endoconidial production.

Buchanan ('11) thought that the spores of the cephalosporium were formed by the abstriction of the tip of the

sporophore, the amount of moisture in the air apparently conditioning the amount of adherence. He regarded as unnecessary the separation of *Hyalopus* and *Cephalosporium* upon the basis of more slime in the former. Studies of *Cephalosporium* spp. on insects led Petch ('28) to agree with Buchanan that the spores were really cut off in succession but became aggregated by the secreted mucilage. In a damp atmosphere some were found in loose chains due to the dissolution of the mucilage. He too disregarded the separation of *Hyalopus* and *Cephalosporium*.

In *Penicillium digitatum* Scaramella ('28) illustrated the rupture of the parent sheath anew below each successive spore. Thom ('10) thought that the spores were merely acrogenous disjunctions which produced their own internal walls and were held together by the phialide wall which did not necessarily rupture until late. This would seem to indicate continued elasticity of the conidiophore wall below the tip. In 1930 he added the following hypothesis regarding submerged cephalosporia:

... that the impulse to produce conidia when acting in a submerged hypha in which all parts are in constant contact with the nutrient, produces a transformed branch bearing spores which tend to enlarge, round up as if for germination, and to lose the catenulate arrangement. This may produce a very peculiar spore attached as a single terminal cell or a cluster of cells not recognizable as conidia and without definite arrangement around the tip of the sterigmatic cell. [p. 73].

Wakyama ('31), in cytological investigations upon *Aspergillus* spp., indicated that the daughter nucleus migrated through a sterigma very similar to the condition in the basidiomycetes, but he did not further investigate the mechanism. Finally Dodge ('35) suggested that the mechanism of conidium formation in the genus *Cephalosporium* is probably close to that of *Aspergillus* and *Penicillium* although the conidiophore is not flask-shaped. If the spores are essentially in chains, they slip past one another very soon to form spore balls.

b. *Previous interpretations of the mechanics of spore production in general.*—There are probably more common factors in all types of spore production than is generally realized, be-



cause the cutting out of similar small masses of protoplasm would not have many physical possibilities of variation. There have been numerous papers regarding this process in the sporangia of the Phycomycetes, a few on ascospore delimitation, and a number on the basidiospore release; whereas, except for Brierley's work, the conidia have generally been neglected.

There are a number of forces which have been championed for spore formation: vacuolation associated with exudation of water or some other liquid; centrosomes or similar bodies which are centers of force and direct the action of protoplasmic streaming; surface tension; Golgi apparatus or the like associated with secretion; and electric forces.

VACUOLES AND EXUDATIONS.—Harper ('99) saw in the sporangium of *Synchytrium decipiens* an early shrinking of protoplasm probably associated with a throwing off of water which accumulated in vacuoles wherein cleavage furrows arose simultaneously throughout the sporangium. In certain cases uninucleate masses were separated, in others multinucleate. He explained the inclusion of a nucleus by the characteristic chemical contents of nucleo-proteins and nucleic acids which were centers of moisture retention or at least had a greater affinity for water than the surrounding cytoplasm.

DeBary ('84) attributed the bursting of the ascus to increased vacuolization due to the absorption of water. In the cutting out of the sporangiospore segments of the Phycomycetes, he mentioned delimiting granular plates which somehow became gelified.

Exuded droplets were shown by Buller ('22) to be significant in the disjunction of basidiospores in all Basidiomycetes except the Gasteromycetes and the Ustilaginaceae. He found droplets also associated with the conidia of the Hymenomycetes and with the aeciospores of the rusts, but thought that such were merely passive. It is possible in these cases too, that, although not effecting violent spore disjunction, exudates may somehow bring about their release. In *Coprinus sterquilinus* he noted that a drop of water 5  $\mu$  in diameter appeared at the base of the basidiospore within ten seconds before its abjunction, and that

the liquid was shot off with the spore and doubtless aided in attaching it to the substratum. It was supposed that the liquid came from the hilum, and was largely water, rather than local mucilagination from the sterigmata (often so narrow as  $0.5\ \mu$ ). The latter, however, must have been ruptured, for it soon collapsed. Buller regarded the production of similar drops in *Sporobolomyces* as suggestive evidence that the genus belonged to the Basidiomycetes in spite of the reduced vegetative growth and completely uninucleate state (Guilliermond, '27). However, Stempell ('35) believed that the water-drop mechanism was merely an ecological response and not of phylogenetic importance. He reported its occurrence in association with both the sporidia and secondary conidia of *Entyloma* of the Tilletiaceae, and also with the sprout cells of *Taphrina*, usually included in the Ascomycetes.

Buller thinks that the hydrostatic pressure of the basidial vacuole is very important in forcing the protoplasm and nucleus through the narrow sterigmata and in the final spore discharge, since the basidium collapsed immediately after the final release of one set of spores: "Now my experience, based upon extensive observations on the living hymenium, is that a basidium never produces more than one generation of spores and that after producing a single crop of spores, its sterigmata and body quickly collapse." [Buller, *l. c.* 2: 28.]

CENTROSOMES, SURFACE TENSION, AND GOLGI APPARATUS.—Maire's ('02) illustration of basidial development in *Psathyrella disseminata* first suggested a centrosomal interpretation of the terminal granules in the imperfects studied. The four centrosomes in the former, produced simultaneously with the four nuclei, situated themselves at the apex and followed the protruding sterigmata with tails of streaming protoplasm ("cordons kinoplasmiques") eventually drawing the nuclei into the spores. These structures, formerly believed to be confined to fungi, algae, and animal cells, are now being discovered frequently in the higher plants. They are apparently centers of energy associated with the action of the spindle in the separation of chromosomes, as well as with the movement

of flagella and cilia, and are generally believed to be absent in the resting cells. There has been controversy over their origin—cytoplasmic or nuclear—and confusion of them with other structures.

Faull ('04) concluded that the centrosomes were of extra-nuclear origin and occurred after reforming of the membrane. Guilliermond, Mangelot, and Plantefol ('33) stated that the centrosome was still an enigma and if it aided in ascospore delimitation, its influence was purely physical, perhaps by the superficial tension on the surface of the asteral parasol which conditioned the formation of new walls. Harper ('99) firmly believed that the aster rays (fibrous kinoplasmic elements) cut out the ascospores and formed the limiting walls. They might well direct the spore delimitation but were themselves included within a special wall, according to Faull ('04). Surface tension and perhaps a different chemical composition kept the endospores discrete from the epiplasm.

Buller ('09), in discussing surface tension and the physics of the jet theory of the ascus, stated that a free cylinder of any liquid under the influence of surface tension became unstable as soon as the length was greater than  $\pi D$ . It is a necessary consequence that if once realized the diameter of such a cylinder will divide into as many equidistant spore lengths as  $\pi D$  is contained in one length. Some such physical interpretation must be necessary for the regulation of the size of the endoconidial segments in the forms studied by the author.

Scarth ('27) thought that a definite structural basis of protoplasm was necessary for life movements. He observed a reciprocity of substance in the increase of mitochondrial elements correlated with the disappearance of the active kinoplasm as a result of vital staining; and concluded that the characteristic component of the chondriome, viz. lecithin, entered into the composition of the kinoplasm, and that the mitochondria merely served as reserve substances for the formation of the more labile elements. Vacuoles were thought to arise from the kinoplasm by the rounding up of fibrillae or as blisters or bubbles from the covering films of the chloroplasts or of the central

vacuole. The wandering streams of protoplasm in the cytoplasm condensed into mucilaginous-looking globules which distended as vacuoles; and an essentially similar process effected the cleavage of coenocytic sporangia. In some cases, however, fissuring arose from fibers that radiated from a central body attached to the nucleus, in others by invaginations of the ectoplasm or by outgrowth of vacuoles. The limiting film of these extensions of the kinoplasm became the plasma membrane of the spores, while the fluid which was secreted between them was presumably analogous to the sap which formed in the vacuole.

Sharp ('34) regarded the divisions by constriction, seen in unicellular algae, in the budding of yeast cells, and in the abstriction of conidia and basidiospores, as special cases of cytokinesis by furrowing. The centriole, or inside of the centrosome, has been generally believed to be a point of high surface tension, and the aster, according to Sharp, might be primarily an expression of streaming movements in the cytoplasm which is somewhat more solid than the rest of the more gelified granular protoplasm. He further said that in the plant cell the furrows probably separated regions of relatively high viscosity even though no aster, in the ordinary sense, was present: "Alterations in surface tension and viscosity, together with protoplasmic streaming, are obviously important factors in cytokinesis of certain types, but comparatively little is known about the initial causes of these phenomena."

Wilson ('25) mentioned the appearance in epithelial muscular and glandular cells of a chromidial apparatus assumed to be extruded from the nucleus and of particular function in trophic actions of the cell. He also thought that there was a definite karyoplasmic ratio which regulated cleavage to produce a fixed or typical cell size at a given stage rather than a fixed number of cells. It was the surface of the nucleus and not its volume that was directly proportional to the number of chromosomes.

The Golgi apparatus is known only in animal cells and is connected with secretion. In goblet cells of the colon, secretory

granules have been said to have originated in mitochondrial (chondriosomal) regions and to have migrated to the Golgi region where they were transformed into mucin granules (Duthie, '33). The granules were then liberated into the cytoplasm, finally dissolved, and passed as liquid secretion into the lumen. This apparatus has also been suggested as a center for the formation of enzymes. Whether a similar process occurs in plants with liberation of mucin has not been investigated. The function and limitations of mitochondria are also disputed questions. Guilliermond ('29) homologized the plant vacuome—which he thought arose *de novo* from the cytoplasm—with the Golgi apparatus and Holmgren canals of animals. Nasonov ('23) believed, on the basis of staining experiments, that the vacuolar membrane had a secretory function and was homologous to the Golgi apparatus.

Weier ('32) thought that the young plastid in spermatogenous, archesporial, and epidermal cells of *Polytrichum commune* and young androcytes of *Pellia epiphylla* showed staining similarities to the animal Golgi apparatus and believed that such might be associated with enzyme secretion, in the former case linked with starch production and in the latter with secretory granules. He did not think, however, that the two should as yet be considered homologous.

Sass ('34) offered further evidence of a Golgi apparatus in the Basidiomycetes, although he failed to associate it with any property of motility as in animals or with the plastidome reported by Weier. The "*nebenkern*" in *Coprinus sterquilinus* was found to divide into four "Golgi crests" which eventually became situated at the tip and presumably cooperated in the formation of sterigmata and in nuclear migrations. These elements resemble superficially the centrosomes of Maire ('02). His results were especially interesting in that he used various new fixatives absolutely free of osmic acid, which eliminated possible errors due to diverse osmophilic substances.

## 2. INVESTIGATIONAL RESULTS

Because in all cases investigated the mechanism of spore formation has appeared to be similar, the results shall be out-

lined in general for the whole group. Plate 1 includes exemplary types selected at random and the figures here mentioned refer to that plate.

The incipient phialide shows a blunt tip which is thicker than the lateral walls and stains darker, be it typically flask-shaped as in *Gliocladium fimbriatum* or essentially straight as in *Cephalosporium niveolanosum*. The dense granular contents do not extend quite to this tip since there is a hyaline area between (fig. 2). A chain of small round granules collect longitudinally, and in fixed preparations show "tails," suggesting rapidly streaming protoplasm (fig. 3). These granules apparently merge into several small rods (fig. 4). Presumably at about this stage a drop of liquid is exuded terminally (figs. 5 and 6); at least in living cultures on hanging drops and agar slides these drops are infrequently noted on blunt hyphae. In the latter material the globule sometimes disappears as it is viewed and runs down the side of the phialide, producing the obviously different appearance of this structure, so often noted, as compared to the rest of the mycelium. In the hanging drops, with low magnifications the downward-hanging fructifications portray cephalosporia with spores literally swimming in the slime which here has not been disseminated by touching the glass. In the next step (fig. 7) a cross-section of the tip shows three granular rods, horizontally aligned, from each of which is a narrow short strip of cytoplasm leading to the protoplast proper. Figure 8 shows a split between four rods which "hold open the sac." The blunt tips seem to be especially resistant at the corners, and the adherence of rods to the sides probably increases this opposition so that the tip swells in the center slightly before splitting.

In the meantime, presumably associated with the exudation of liquid, the contents of the phialide have cleaved into a varying number of segments which at first are noted as regularly occurring cross-lines of granular dark-staining material, indicating regions of high surface tension. Later, narrow hyaline areas appear between the segments which round up at the edges. At the very base of the phialide are a varying number of small vacuoles. The spore, clad only in a fine membrane, be-

gins to protrude from the rigid collar of the phialide whose narrowness considerably retards the process (figs. 9 and 16). As if forced out by pressure from the increasing vacuoles at the base, the spore becomes somewhat constricted, as indicated by its tendency to round up on emergence, and causes the included end to become increasingly convex. Finally, after the greater part has emerged, the rest of the spore snaps off, and is immediately followed by a successor. This process is relatively slow, under optimum conditions only three spores being emitted from a phialide during seventy minutes (fig. 17). The exuded slime and the moist surface of the spore hold it near the phialide. In the spore ball it cannot escape until moisture disseminates the mucilage. Very thin sections of paraffin material seem to indicate that the spore is abstricted as is the yeast bud (fig. 15). This appearance may be explained by assuming that one of the granules at the tip really stays in the center of the phialide and draws the cytoplasm as a narrow stream into the spore; and in some thin sections it is impossible to see any lateral granules. Moreover, young phialides show blackish regions at the tips which probably represent central granules.

Since the greatest diameter of the phialides averages only  $2\mu$  and the contents are granular, it is impossible to make out nuclei in the celloidin material, but in the thinner paraffin sections each cell and endoconidial segment appear to be uninucleate. The energid is but slightly larger than other dark-staining metachromatic granules throughout the cytoplasm. No definite mitotic stages were espied. The fine stream of protoplasm passing into the spore stains very darkly, perhaps due to a passing nucleus or to compression and rapid streaming. Sometimes mature spores show numerous refractile granules, at other times a more definite accumulation which is regarded as a true nucleus. After emergence, the spores form a thin wall around the membrane, swell doubly or triply, and germinate after several days. In some cases they appear to be germinating while still within the ball (pl. 5, fig. 16). Since the mucilage swells upon the addition of water, when favorable moisture conditions occur the spores are released both for dispersal and germination. In the meantime, they have been

protected by the slime. Thus cytologically the conidia in these species are haploid representatives of haploid individuals, apparently capable of indefinite existence without fertilization.

While the spores are being released the vacuolar area within the phialide multiplies conspicuously. The latter is increasingly contorted and devoid of protoplasm (especially noticeable in the larger single conidiophores of *Clonostachys Araucaria*). Doubtless, the vacuolar force, as well as the mechanical one of twisting, aids in the liberation of the spores. Neither by differential staining nor polarized light were any essential differences in the chemical nature of the phialide and ordinary mycelium observed.

Young tips of ordinary hyphae were more clearly observed in hanging drops than on agar. They are always more or less pointed and of the same consistency as the rest of the wall. Vacuoles extend quite close to the apex and contain one or several very active and large dancing bodies (pl. 3, fig. 21). Buller ('33) mentioned highly refractive particles (Woronin bodies) in *Ascobolus pulcherrimus*, on both sides of the septa and in terminal cells in a dispersed condition. In older cells they were said to settle down in the walls of the vacuoles, never in the protoplasm proper, and were associated always with the sap cavity, even passing through septa with it. These may be identical with the large dancing bodies, or even the larger septal granules (pl. 3, fig. 20), although the author does not think the latter two are the same. In fact, there seem to be dancing bodies which appear dark even *in vivo*, and cytoplasmic granules which show only in fixed preparations. The crowded vacuoles with small metachromatic granules visible between them soon occupy approximately the whole cell except for a narrow peripheral layer and a cytoplasmic region in the center where the nucleus is hung (pl. 3, fig. 19). Around all aerial hyphae on agar slides was noted a fine layer of mucilage, which indicates that apparently such exudation is normal in the life of the organism, and differs only in quantity in the phialide.

For comparison, a cursory examination was made of living material of *Scopulariopsis brevicaulis* (Sacc.) Bainier, a



species whose spores are held together in chains by disjunctors. The process agrees very well with that shown by Scaramella ('28) in *Penicillium digitatum* Sacc. The terminal uninucleate segment puts down an internal wall as a chlamydospore does, and by its swelling ruptures the external wall at the shortest diameter of the ellipsoidal spore which remains adherent at the base and connected with the rest of the phialide. This leaves empty a lens-shaped connective between the chain of spores abjoined similarly and successively. Meanwhile, there has been a slight cleavage of the protoplasm into a number of segments within the phialide, so that although only one spore becomes encysted at a time the potential ones are already present as in the phialide of the cephalospore. The main differences in the latter are the lack of resistant spore walls and method of rupture of the phialide, whose functions, as well as that of the disjunctor, are taken over by the mucilage. Comparative cytological data would be interesting.

### 3. INTERPRETATION

It seems probable that the incipient phialide eventually forms a rigid tip which is no longer capable of stretching and of intussuscepting material. The contents of the cell are continually swelling due to vacuolar as well as osmotic pressure and to surface tension, indicated by accumulation of granular material which eventually causes a rupture. In the meantime the granules have strengthened the corners so that the middle of the tip is stretched and broken and the size of the opening is considerably narrowed. The exudation of the mucilage, whether effected by the granules or not (though such seems likely, and it must come from the living protoplasm itself), doubtless makes possible the cleaving of the protoplasm as has been suggested in the basidium and sporangium. Whether the terminal granules represent centrosomes or Golgi bodies, the author is not prepared to state; but at any rate they must represent kinoplasmic elements similar to those of Scarth ('27). They may be an aggregation of chondriosomes whose significance is not clear.

Further, the mucilage production may be compared with guttation in the angiosperms (Wilson, '23), where there were found 220–1030 ppm. of organic material, mostly nitrates and nitrites, in the exudate. This indicates that occasionally colloidal material can be passed through intact walls. The terminal wall was not broken in the phialide at first, since it was sometimes visible within the droplet. The theories that the slime arises from between the membranes, as suggested by Knoll ('12) in cystidia, or by deliquescence of the middle lamellae (Brierley, '15) or of spore walls themselves (deBary, '84), are plainly inapplicable here.

Granules such as those occurring terminally in phialides are not noted in the ordinary mycelial tips, although similar (?) ones (pl. 3, fig. 20) are discernible in ordinary cross septa, perhaps exercising a function associated with the protoplasmic connectives.

The cleavage itself is largely a surface tension phenomenon and is doubtless often only partial, i. e., the cleaved parts occur only in small numbers towards the tip of the phialide and this process may be repeated; hence all the nuclear divisions do not have to take place at once. Such is exemplified in embryological studies of cleavage of animal eggs. Possibly, due to the water-holding capacity of the nucleus, liquid is exuded equidistant between the energids where increased surface tension is noticeable in fixed material by a layer of basophilic granules. Buller's physical theory would explain the size of the segments (cf. p. 10 of the present paper). The spores are released by the vacuolar pressure in the lower part of the phialide. Cohesion and surface tension factors, associated with a narrow rigid opening and the tendency of an elastic portion of a spore to round up when the pressure is released, assist the process. The size and shape of the spore are doubtless dependent upon the extent of the phialide and its opening as well as upon the amount of cytoplasm included in the endoconidium, all being explainable upon a purely physical basis. That the species of *Cephalosporium* have the longest narrowest spores is due to a comparatively straighter phialide which makes the endoco-

nidial column more extensive. Extrusion thus takes longer, and the membrane or new cell wall becomes more or less rigid before the spore is completely released.

The purely physical force of pressure must also be assisted by that of twisting caused perhaps by spiral streaming of the protoplasm. Although the author has seen no previous mention that this force assists in spore dispersal, Castle's ('34) reference to it in growth is suggestive. He states that the twisted or helical forms of growth are generally due to the resolution of two growth vectors: one longitudinal and one rotational. Oort ('31) had measured simultaneous growth and twisting along the axis in the coenocytic spore-bearing cells of *Phycomyces* and found at 17.5° C. an average rate of elongation of 39  $\mu$  a minute and an average rate of rotation of 3.7 degrees a minute. The angle at which micelles were incorporated in the wall was about 6 degrees. The steepness of the growth spiral was not structurally fixed but was reversibly altered (reversed or abolished) by change of temperature. The majority of the cells grew in the form of a right-handed helix, i. e., left-handed thread on a screw. The rapidity with which the angle of coiling changed seemed to refute the interpretation of altered proportions of different types of isomeric molecules. It may be that spiral streaming of protoplasm helps in the phialide twisting, but this is purely conjectural since no proof has been obtained.

The eventual collapse of the phialide results from the lack of compensating turgor pressure from the end wall which has become open (also an aid in the spiral twisting). Such a condition is less noticeable in the typical penicillate fructifications which have the most minute openings, especially in comparison with those of the rest of the phialide, than in the broader, straighter, and simple ones of *Clonostachys Araucaria*. If the spores were merely produced acrogenously there would be no exhausted remnant; moreover the endogenous condition here is more similar to that in the basidium and less like that in the ascus because there is no residual epiplasm.

The slime forms a protective covering around the delicate

thin-walled spores until optimum moisture conditions arise, when it not only makes the spores available for germination but also causes considerable dispersal due to the colloidal swelling accompanying its solution in water. Because of this miscible property the amount persistent around the spores will depend upon the humidity of the atmosphere. In very dry conditions the external layers tend to become almost rubbery, as ascertained by Cooke and Ellis ('78) in the solid slime balls on herbarium specimens of *Penicillium repens*.

The submerged cephalosporia of *Cephalosporium Serrae* appear to be homologous with the aerial ones except possibly for a greater tendency to irregularity in shape due to the confining action of the medium. In *Torulopsis mucilaginosa*, on the other hand, the whole growth is obviously a budding pseudomycelium and actual production of endoconidia was not observed. In *Cephalosporium symbioticum*, the cephalosporia attached to the short laterals more nearly simulate the fructification of *Allescheria Boydii* than that of *Cephalosporium*. Since this condition occurs in *Torulopsis mucilaginosa* only in submerged growth, it is an abnormality, and whether it may indicate a foreshadowing of the conditions in the regular forms or a reversion from an advanced to a reduced type (the yeast) is still a question. The latter view is the more logical.

In agreement with Wakayama ('31), the present data indicate that the conidiophore is an asexual organ of the haplont producing uninucleate spores which repeat the life cycle without variation except for secondary asexual spore forms. The occasional conjugation of conidia is without significance so far as is known.

#### B. OTHER CONIDIAL FORMS ENCOUNTERED

Omnipresent in this group are terminal or intercalary chlamydospores whose new cell walls are put down inside the parent cells. The production of chlamydospores is ordinarily associated with adverse conditions, and dissemination occurs when the adjacent cells die. Besides these, in *Gliocladium fimbriatum* and *G. deliquescens* large terminal cells rich in oil

droplets are formed, which differ from chlamydospores in their relatively thinner walls and capability of immediate germination as evidenced in hanging drop cultures. For such, the designation akinete has been adopted from algological terminology. Moreover, there are noted within the medium enlarged round to ovoid terminal cells beyond which the hypha may grow again (pl. 3, fig. 30). Their subsequent development was not followed, but when observed they were thin-walled. They may possibly be aborted ascogonia, and Thom has referred to them as due to the same impulse as that causing submerged cephalosporia. If they function as chlamydospores, at least their method of formation is somewhat irregular.

The peculiar short-stalked spores produced promiscuously over the terminal clubs in *Clonostachys spectabilis* cannot be discussed in detail since the culture died early, but they are obviously not comparable to the other forms studied. A superficial resemblance between spores and the warty structures of the phialides of *Clonostachys Araucaria* may have caused Oudemans ('86) to include that species in *Clonostachys*. However, the warts are not spores but thickenings on the wall, not uncommonly seen in fungi and are incapable of germination.

Infrequently oidia were noted in *Gliocladium Vermoeseni* (pl. 4, fig. 11). The significance of these secondary spore forms is obscure. If such occur in *Penicillium* and *Aspergillus*, Thom ('26, '30) did not mention them, unless the "hülle" cells first cited by Eidam ('83) in some species of *Aspergillus* could be considered such. It is obvious that hyphosporic types of spores are produced in response to unfavorable conditions, especially where the colony has exhausted the medium and an indefinitely resting spore is needed.

#### IV. PHYSIOLOGY

##### A. COMPARATIVE CULTURAL CHARACTERISTICS

In table 1 are listed most of the organisms studied on a representative number of media, with brief notes regarding color, surface, and microscopic characteristics. Some correlations





TABLE I  
COMPARATIVE CULTURAL CHARACTERISTICS IN VARIOUS MEDIA

Nitrite pH 5.5	Campak pH 4.48	Potato dextrose pH 5.7	Corn meal pH 6.0	Gordouche-Manuel pH 6.8	Sabouraud's dextrose pH 5.6	Lactose broth pH 6.8	Sabouraud's Conservation pH 7.0	Glycerine pH 6.9	Carrot plug
Gull gray, powdery, sub-merged; single spores.	Gray-white, flat acaul.	Gray-green, black below wrinkled; cornea; an- gle spores.	Gray, powdery; single spores.	Orange, flat, mottled, filamentous; single spores.	Pale gray, long, fuzzy; many single spores.	Gray pellicle of small re- sulting colonies.	Gray-violet, black, flat, powdery.	Dark gray, corrugated; single spores.	Gray-green, short, fuzzy.
Apicot-luaf, conchiform; chlamydospores; sub- merged cephalosporia.	Orange, rough, hooped, edges submerged.	Deep orange, furrowed; cephalosporia; clammy spores.	Pale pink; submerged; chlamydospores and cephalosporia.	Pale pink, flat, mottled, sterile.	Pink, corrugated; cor- neal; small cephalospo- ria.	Pink ring, liquid turbid.	Pink, moist, much wrinkled.	Strawberry-pink, slightly wrinkled; many cor- neal.	Pink, tallows, with radi- ating cornea.
Slump-pink, flat, wrinkled; chlamydospores; radi- ating cephalosporia.	Bluish-white, flat, with radiating striations.	Yellow-white, hooped in center, hairy prope- rium, sterile.	White, wrinkled; many cephalosporia.	Pale tan, hooped, hairy protrusions; clammy spores.	White, corrugated; cor- neal; small cephalospo- ria.	White yeasty ring, slight turbidity.	White, round elevated con- ters and spreading lath.	Snashel pink, rope-like, with cornea.	White, tallows-like; few cornea.
Orange-pink, flat, corrugated; submerged cephalosporia.	White, edges submerged; hairy cottony.	Coral pink, corrugated; few cephalosporia.	Deep pink, flat, moist; cephalosporia.	Pale pink, wrinkled, much submerged, sterile.	Pink orange, flat, moist; few cephalosporia.	White ring, slight turbid- ity.	White-silvery, hard cere- bral colony.	Frosted seashell-pink; radiating, many cephalosporia.	White, tallows.
Gull-gray, short-flores- cent, at center; many spores and cephalospo- ria.	White, hooped, rough, edges submerged.	Sludgy gray, many clammy droplets; few cephalo- sporia.	Silvery-gray, powdery; much submerged clammy spores; few cephalo- sporia.	Gray-powdery, flat with black; chlamydospores.	White, moist; some cor- neal; few cephalospo- ria.	Downy white pellicle.	Yellow, powdery top, wrinkled.	Pale pink, cottony, slightly wrinkled.	White, tallows, some fuzz, some cornea.
White, short, rough sur- face submerged; many cephalosporia.	White, flat, granular, im- bibe.	Pale pink; nodular cor- neal; many cephalo- sporia.	Pale pink, slightly ele- vated, dry; many cephalo- sporia.	Opaque, round elevated, radial furrows, sterile.	White, moist; some cor- neal; few cephalospo- ria.	White yeasty ring, tur- bidity.	White, hard, wrinkled shell, orange below; cornea.	Pink, wrinkled below; cor- neal.	White, tallows.
Pale pink, mostly sub- merged; few cornea; many cephalosporia.	White, mostly sub- merged; few cornea; many cephalosporia.	White, mottled with pink chlamydospores; sub- merged cephalosporia and chlamydospores.	White, mottled with pink chlamydospores; sub- merged cephalosporia and chlamydospores.	Pink, flat, wrinkled; sub- merged cephalosporia and chlamydospores.	White, moist; some cor- neal; few cephalospo- ria.	Yellow-green pellicle; pink submerged hyphae.	Pink then black, mostly submerged; cephalospo- ria and chlamydospores.	Orange cornea and pink- ish; cephalosporia and chlamydospores.	White powdery.
Citron, in medium too, powdery, submerged; rare acaul cephalospo- ria.	White, slightly raised, granular center, orange below; cephalosporia.	Pink, cottony; many chlamydospores; few cephalosporia.	Pale pink, scattered, small dry bags; cephalospo- ria; chlamydospores.	Copialosporia.	Pale pink, dry, powdery; many cephalosporia.	Powdery white pellicle, some hyaline basal growth.	Pale pink, cottony; cephalosporia.	Slump-pink, downy um- brella, wrinkled below.	Pinkish-white, short- haired fuzz.
Prunel-yellow, in me- dium submerged; few merged; few acaul cephalosporia.	White-pink, discrete mottled colonies; few cephalosporia.	Clauky white, hairy, flat, mottled growth, sterile.	Orange, flat; cephalospo- ria.	Clauky white, mottled center; chlamydospores; cephalosporia.	White, moist; some cor- neal; few cephalospo- ria.	White, yeasty ring, slight turbidity.	White, yellow below, wrinkled.	Pink center rough hairy; wrinkled below; cephalo- sporia.	White, small spores growth.
Orange-pink, powdery; cephalosporia.	Pink, raised, fuzzy.	Pale pink, flat with pow- dry tufts; cephalospo- ria.	Pink, scattered tufts; cephalosporia.	White, rough, mottled; cephalosporia.	Pale pink and white, downy.	Pink-white, powdery pol- low, wrinkled.	White, mottled, yellow be- low, wrinkled.	Pink-orange, thick-mat- ted, wrinkled below; few cephalosporia, avo- lan thin-walled cells.	Pink, fuzzy, good growth.
White, green dots, mostly submerged scattered threads.	White, fuzzy; submerged cephalosporia.	Blackish-green, medium brown; acaul cephalo- sporia.	Green dots scattered; spores growth; loose spores.	Sterile.	White; many cephalospo- ria.	Gray-green surface pel- licle hyaline below, h- airy, mottled, orange cells; an cephalosporia.	White cottony center; cephalosporia at edge.	White cottony center; cephalosporia at edge.	Delicate green fuzzy growth.
Dark green, medium yellow; submerged cephalosporia and acaul spores.	Dark green, white edges; cephalosporia.	Deep green, medium tan center; many cephalosporia.	Green, moist; many cephalo- sporia.	Yellow-green, powdery, moist, cephalosporia.	White, medium yellow- green, cottony.	Pale green, feathery, rad- ial hyaline in liquid too.	Medium green, edges white, rapid flocculent growth, medium olive- yellow; many cephalo- sporia.	Medium green, edges white, rapid flocculent growth, medium olive- yellow; many cephalo- sporia.	White hairy growth.
Pink powdery; many cephalosporia.	White, sparse mycelia; pink cephalosporia.	White, spores; chlamydo- spores; submerged cephalosporia.	Pink, powdery, elevated; few small cephalospo- ria.	White, powdery, sterile.	Transparent, scattered.	Pink ring, liquid clear.	Pink spore balls, white cottony hyphae.	White mycelia; lavender spores; rapid growth.	No growth.





may be drawn here, indicating as favorable media the glycerine, Sabouraud's dextrose, and Czapek's agars; and as unfavorable, nitrate and Gorodkova-Maneval agars; as less so, corn meal and potato-dextrose agars, carrot slants, and liquid media. Growth on the first group is typified by abundant large, aerial mycelia with comparatively few types or numbers of spore forms, deeper internal coloring with little if any exuded pigment, much guttational water, and a convoluted colony. Unfavorable conditions are recognized in sparse surface growth of long slender filaments, a tendency to submerged mycelium, relative increase in reproductive bodies such as chlamydo-spores, conidia, and coremia, dry powdery growth, paler or tending toward yellow rather than orange pigmentation endogenously, with frequent exogenous coloration of the medium.

In the next section some of the prominent factors and theories for cultural deviations which seem especially applicable in the case at hand will be more fully discussed.

#### B. FACTORS INFLUENCING MORPHOLOGY AND PHYSIOLOGY

Of the numerous variables possibly relevant, the present discussion is limited to hydrogen-ion concentration, surface and oxygen tensions, and kinds of nutrients. Temperature, doubtless influential, will not be considered, since all were grown at 30° C.

1. *Hydrogen-ion concentration.*—It must be remembered that the hydrogen-ion concentration refers to the relative acidity or percentage of dissociation as contrasted with the total acidity; although the latter factor, as well as the chemical nature of the acid itself, also influences growth. Moreover, microorganisms contain natural buffers and have to a limited extent the power to adjust the pH of a medium toward the optimum as a result of their activity.

The media utilized covered a wide natural range of H-ion concentration, from Raulin's (pH 4.15) to Endo's (pH 7.5), with growth upon all. An artificial series from pH 3.8 to 7.6, maintained upon glycerine agar (table II), gave the most striking results in the tendency towards submerged growth at the

higher concentrations of pH. At pH 4.4 and below and at pH 7.6 the media did not solidify. It is interesting that *Gliocladium deliquescens* grew in the liquid at the higher acidities, but formed a pellicle at the higher alkalinities. On the other hand, *Torulopsis mucilaginosa* grew extensively and normally upon wort agar (pH 4.8) but with mainly submerged cephalosporia upon nitrate agar (pH 5.5); whereas the true molds showed an inundated state upon the latter and abnormal aerial conidiophores even upon wort.

Organisms listed as *Monilia albicans* have been extensively used in physiological studies. Marantonio ('93) stated that at the higher acidities there was a greater quantity of mycelium; and that there was a tendency to filamentous growth on liquid, with sprouting almost exclusively upon solid media, or hyphae only on old cultures. According to Fineman ('21), mycelial growth was better under low surface and oxygen tensions, but the yeast form predominated upon solid media, simple carbohydrates, and a low acidity. Mallinkrodt-Haupt ('32) stated that the yeast form predominated in a strongly acid medium, whereas the filamentous occurred in a very alkaline one; and he also mentioned that H-ion concentration influenced the metabolism, enzyme actions, morphology, toxin production, and immunological characteristics.

Buchanan and Fulmer ('28) found that some of the molds could tolerate a range of pH from 1.6 to 11.2, but that there was an optimal section with atypical growth deviations on either side. With fermenting yeasts alcohol was formed under acid conditions, and glycerol as an intermediary under alkaline ones.

In *Endomyces capsulatus*, Moore ('33) said that in acid media the tendency was towards abundant budding, numerous conidia, and longer narrower cells; contrarily, on alkaline substrata there was an inclination towards shorter thicker cells with yeast-like formations and fewer conidia.

Hewitt ('33) said that the pH had an effect upon the oxidation reduction system, which resulted in an alteration of the ionic equilibria. Clark ('22) thought that the H-ion concentration functioned chiefly as a conditioning agent and was only in-

TABLE II  
EFFECT OF HYDROGEN-ION CONCENTRATION—GLYCERINE AGAR

Organism	pH 3.8	pH 4.4	pH 5.0	pH 6.0	pH 6.4	pH 7.0	pH 7.6
<i>Allescheria Boydii</i>	No growth.	No growth.	Gray, velvety, somewhat submerged, wrinkled.	Very slight growth.	Gray-velvety growth.	Luxuriant gray down, black center, moist.	No growth.
<i>Clonostachys Aracuaris</i>	No growth.	No growth.	Fine mycelium, pink, powdery; one coremium.	Pink, fluffy, powdery.	Pink and white down, wrinkled, moist.	White down becoming pink, powdery, dry.	No growth.
<i>C. Aracuaris</i> var. <i>confusa</i>	Slight growth.	No growth.	Pink-orange, powdery; few coremia.	Pink, cottony, quite coarse.	Very cottony and pink, moist.	White then salmon, downy.	Small amount of submerged growth.
<i>Cephalosporium Serrae</i>	No growth.	No growth.	Pink, coarse growth, soon becoming black with chlamydo-spores.	Heaped compact colonies.	White, wrinkled, cottony; coremia.	White, tufted.	No growth.
<i>Glodadium deliquescens</i>	Submerged growth; cells thin-walled, granular, short, contorted, with intercalary ones of swollen walls; no cephalosporia.	Colorless growth in liquid; cells less contorted and longer, granular; some cephalosporia.	Mostly submerged growth, white with green dots.	Fine white surface growth with green slime balls, aknetes; cells long and narrow, heterogeneous contents.	Flocculent white growth with green slime.	Flat dull surface growth and somewhat submerged.	Heavy pellicle and radiating hyaline hairs; cell walls thick, hyaline, contents granular; few terminal chlamydospores; no cephalosporia.

directly concerned with chemical transformations closely related to life processes.

2. *Surface tension*.—Surface tension is the cohesive pull of the internal and adjacent molecules upon those of the surface layer. It is particularly important in the life of the organism in relation to adsorption and absorption. This tension produces surface energy, which, unhindered, effects the assumption of minimal surface for a given volume, i. e., a sphere. At the interfaces which are sites of chemical and physical activity, surface tension is constantly being opposed. Anything causing a lowering of surface tension will permit a larger surface; for example, mycelial growth will be favored, but under the other condition the cell size will be limited and yeast-like proliferation result. The appearance of filamentous forms in liquids is probably a reaction due partly to surface tension, and represents unfavorable adaptation to an unfamiliar substratum.

Artificial reduction of surface tension has been secured by Fineman ('21) with the addition of sodium ricinoleate to a medium with dextrin solutions, but not those containing galactose. Glycerine has also been found to lower surface tension and increase mycelial growth. Upon the basis of similar observations, Czapek ('11) was led to stipulate the necessity of lipoids in the surface membrane. Surface tension is greatly affected by the polar orientation of interfacial substances, the amount of ionization, and the pH (which determines the basic or acidic activity of amphoteric proteins).

Larson ('21) attributed his success in growing normal pellicle-forming bacteria on the bottom and vice versa by lowering or raising surface tension, to the non-wetting properties of the lipoids in the surface pellicle. Buchanan and Fulmer ('28) reported similar results in making *Clostridium tetani* grow superficially, but they suggested that the surface-active solutes concentrated in the surface boundary might also cut down the solubility of oxygen. They also mentioned the tendency of *Bacillus subtilis* to sporulate in media of low surface tension. Oxygen tension, availability of nutrients, etc., may overbalance or at least modify the effects of surface tension.

3. *Oxygen relationships*.—The aerobic and anaerobic states are dependent upon the oxygen relations. Topley and Wilson ('29) stated that anaerobes were not supersensitive to oxygen itself, i. e., that oxygen was not toxic, but that hydrogen peroxide was produced abundantly in the presence of free oxygen for whose destruction no catalase or equivalent system was present. This theory also explains why anaerobes can sometimes be cultivated with an aerobic form in air, the latter destroying the peroxide.

Fineman ('21) found mycelium formed in *Monilia albicans* on surface agar slants cultured in carbon dioxide. The usual correlation of budding and high oxygen tension and of mycelium and low oxygen tension was noted, but there were exceptions. According to Fuchs ('26), reduced oxygen tension favored sporulation in yeasts. Dodge ('35) stated that lowered oxygen tension favored hyphal production to some extent.

The metabolic relation to oxidation is also intimately associated with the substratum. Stephenson (Buchanan and Fulmer, '28) found the normally aerobic *Bacterium coli* (*Escherichia coli*) developing anaerobically during the first stages of glucose breakdown, and thereafter aerobically. However, if grown in pure oxygen it utilized such from the beginning, nor was there any increase in the ratios of glucose decomposition, but the active metabolism persisted longer than in the former case and the acidity increased more slowly. Thus the apparent effect of the increased oxygen was to induce further breakdown of some acid product of the fermentation of glucose. An increased oxygen tension accelerated the respirational rate when dextrose was replaced by ammonium-lactate, and made possible the derivation of carbon from salts of acetic or succinic acids but under aerobic conditions only. In a synthetic medium of simple organic acids (such as lactic, succinic, fumaric, or pyruvic) to which nitrate was added, the organism could grow anaerobically by utilizing the reduced nitrate as a hydrogen acceptor or oxygen donator. Buchanan and Fulmer ('28) further noted that in *Bacterium coli* (*Escherichia coli*) and *Clostridium Welchii* smaller amounts of carbon dioxide were produced aerobically than anaerobically.

Hewitt ('33) offered an explanation of aerobiosis and anaerobiosis on the basis of oxygen-reduction potentials in place of the view that anaerobes have no catalase. He showed that aerobes (such as staphylococci, streptococci and pneumococci) reduced the broth medium whereon they were cultivated, which had an initial potential of almost  $-0.3$  volts, to as low as  $-0.15$  to  $-0.20$  volts. Anaerobes, on the other hand, could not begin growth on such a medium, but with pieces of meat in the broth the potential became reduced to  $-0.2$  volts, due to a reversible oxidation-reduction system therein. Such potential was not changed by staphylococci which had reached their minimum, but was lowered by anaerobes to a limit of  $-0.4$  volts. The preliminary reduction of the medium might be effected artificially by four methods: (1) hydrogen in an anaerobic jar, (2) pure nitrogen, (3) various chemical-reducing agents, (4) growth of aerobic organisms.

4. *Kinds of nutrients*.—Besides the above-mentioned interrelations of oxidation and nutrient necessities, there have been some definite observations regarding the nature of the latter alone.

Talice ('30), in his extensive study of media and conditions favoring the formation of hyphae, found that mycelium was formed the first few days and then mainly yeasts, with the filamentous form only in contact with the agar surface. Surface tension may enter here and oxygen phenomena, since the inside of a colony is under reduced oxygen pressure. He noted that normal yeast forms produced hyphae with dextrin peptone media or glucose, and to a lesser extent with protein. Incidentally, he regarded the yeast state as a senescent one.

Plaut ('13) found yeasts in sugar-rich media and mycelia in sugar-free nitrogenous substrata. Buchanan and Fulmer ('28) spoke of the "protein-sparing" effect of dextrose. Topley and Wilson ('29) thought that there was no such effect, but rather an inhibition of bacterial growth, due to the rapid increase in hydrogen-ion concentration of those media containing a fermentable carbohydrate.

Further conclusions have been drawn from work with *Monilia albicans*. Roux and Linossier ('90) stated that the com-

plexity of morphological structure increased with the molecular weight of the food elements, i. e., yeasts in simple sugars, and filaments in complex carbohydrates. Such statements have not been fully confirmed. According to Mallinkrodt-Haupt ('32), the yeast form appeared in the tissues of the host, but in culture the mycelial one. Discordantly, Fineman ('21) reported both conidia (yeasts?) and mycelium in the host, but only the one or the other in culture. No explanation was offered but if such be true, the heterogenous nature of the internal environment may be responsible.

5. *Discussion.*—It soon becomes obvious, when trying to check physiological causes and effects, that there are many variables concerned, making it practically impossible to attribute a definite reaction to one alone. Nevertheless, some likely influences can be designated.

There is an optimum range of hydrogen-ion concentration between pH 5 and pH 7, and the best is around pH 6.4 for the majority of these forms. Below and above the range the growth is restricted and the relative number of reproductive bodies, especially chlamydospores, augmented. Moreover, the maladjustment is exemplified by atypical colony characters—i. e., submerged contorted growth at the higher acidities and aerial if scanty growth with increased alkalinities.

The forms studied show strong aerobiosis, tending to form pellicles on liquids, but are occasionally submerged with modified hyphal growth due to other more influential causes. If other conditions are unfavorable, however, all of the organisms may grow immersed even on a solid substratum. These molds seem to require media rich in both carbohydrates and proteins. The organic nitrogen foods are more easily assimilated than the mineral salts; and sugars better than starches. Glycerine is readily utilized.

Some of the present results may be explained as follows: the relative acidity may occasion the submerged growth in Czapek's medium; low carbohydrate supply in nitrate and Gorodkova-Maneval agar necessitates the utilization in the first case of nitrogen of a mineral nature and in the other of an organic nature, with comparable results; utilization of com-



plex plant carbohydrates *in situ* in corn meal, potato, and carrot, with increased production especially of coremia; strong aerobic tendencies evidenced by heavy pellicle, with the species of *Cephalosporium* best able to grow anaerobically if atypically submerged.

Although some have regarded the yeast type as a senescent primitive form (Talice, '30), present evidence would seem rather to indicate a reduced type. The yeast has become a highly specialized saprophyte, i. e., adapted to growth in sugar solutions. Such a habitat has effected extreme morphological changes which caused sexual degeneration, and the almost exclusive assumption of the budding state due probably to chemical and physical causes associated especially with surface tension and the nature of the substratum. Perhaps the status of oxidation-reduction potential in the sugar medium may elucidate upon the morphological effect. Hewitt ('33) lists carbohydrates as having an unknown reversible oxidation-reduction system.

The insertion of the yeast stage normally in a filamentous form is interesting too. For example, the smut sporidia propagate rather indefinitely by budding. Conidia of the *Plectascales* have also been found upon occasions to bud for various time intervals. Fuchs ('26) gave a review of the early concepts which regarded the sprouting interval as a part of the life cycle of filamentous forms. He found that *Aspergillus Oryzae*, especially on wort and wort gelatine, remained permanently in the yeast stage. Such data have not been duplicated to the knowledge of the author. The latter media have been found unfavorable to the molds, probably because of the large amount of sugar, reduced proteins, and also relatively high acidity. In pseudomycelial forms—*Monilia* in the general sense of the name—the yeast state is prevalent under favorable conditions, and the mycelial one under unfavorable situations according to Henrici ('30).

#### C. COLOR

The two dominant colors found in this group are green and red in various shades, although one organism was gray and

three were sporadically yellow. The first pigment seems quite constant under all conditions and is apparently in the mycelial protoplasm as well as the spores. In *Gliocladium deliquescens* optimal growth shows almost complete covering with a green slime whose color is doubtless due to the numerous spores included. *Gliocladium penicilloides* generally is chalky-white, but sometimes becomes pale yellow and on glycerine agar exudes the same pigment into the medium. A similar condition is present in *Clonostachys Araucaria* and its variety *rosea* on nitrate medium. The pigment is water soluble.

It is the various red and orange shades which attract particular attention. The pink pigment of *Gliocladium Vermoeseni* is obviously contained within the spores since the mycelium is a white flocculent growth. In the species of *Cephalosporium* the pigment is dispersed within the mycelium, but its intensity or mere presence is conditioned by varying factors of light, temperature, substratum, oxygen relations, associated probably with general metabolism. A few observations are to be mentioned here, although little experimental work was done upon their nature.

*Cephalosporium kiliense* when growing most luxuriantly in the light is a rich apricot-orange; but as the culture stales, or on media low in accessible nutrients, or in the dark, it fades to a pale yellow-orange or even almost white. *C. niveolanosum* is a paler pink at best and is white if kept in the dark (at the same temperature) for even a few days. The color of the *Torulopsis mucilaginosus* is more persistent, but in one case when a culture was placed in the refrigerator (13° C.) for two months it became white and remained so on all subsequent transfers.

An attempt was made to extract the pigment of *Cephalosporium kiliense* with various solvents. With concentrated sulphuric acid the specimen became blue-green immediately, and the liquid later had a cherry-wine color due perhaps to the dissolution of agar. Concentrated hydrochloric acid turned the solution a blue-green color which faded to yellow. Fuming nitric acid, as well as 20 per cent sodium hydroxide, dissolved the fungus and medium with no color reactions. There was slight solubility in chloroform as well as in hot 95 per cent

alcohol and in lactic acid. Entirely ineffective were petroleum ether, benzol, oxalic acid, salicylic acid, acetone, formaldehyde, and ethyl-ether. The pigment was especially soluble in acetic acid and upon evaporation yielded a yellow-orange mass which appeared amorphous under the microscope. This observation is insufficient to identify the pigment, although it seems related to xanthophyll. The reaction with hydrosulphuric acid was not the typical one of lipocyanin.

Color variations have been occasionally noted in fungi, and Zopf ('90) worked out some rather complicated methods of extraction and determination. Palmer ('22) stated that in some cases the reds and yellows were doubtless due to carotinoids, whereas in other cases they were not, as in chrysophanic acid. Pigments have also been cursorily noted in the bacteria, and it has been possible to separate rather constant strains, and at other times conspicuous color variants have been noted in a colorless colony or vice versa. Little or nothing is known of the chemistry or physiological purpose of pigments. Some theories have been promulgated: reserve of oily nature in the rust spores (Zopf, '90), a protective function to cellular enzymes (Went, '04), and an oxidation pigment. It may be that the pigmentation is largely associated with conditions of acidity and alkalinity in the medium, as Thom ('26) has suggested, yellow occurring in acid conditions and red in alkaline.

In the cases at hand—*Cephalosporium niveolanosum* and *C. kiliense*—it is possible that the pigment is a reserve and indicates excessive anabolism, but chemical investigation would be necessary to substantiate the view. A protective function seems quite logical whether for enzymes or the cytoplasm itself. The association with respiration seems unnecessary, since existence is possible without pigment in these species and in closely allied ones (e. g., *C. rubrobrunneum* and *C. Stuehmeri*, separated almost entirely upon the presence or absence of pigment). At any rate the problem is still an open one and possibly full of significance.

According to Henrici ('30), the pigment production in *Actinomyces* was more constant and also more striking in media of rather low nutrient value, which is the reverse of the present

findings except for *Clonostachys Araucaria*, where abnormal pigments are released in the medium. Colley ('31) enumerated changes in color of *Serratia marcescens* and *Azotobacter chroococcum* upon the addition of certain salts to Bacto-agar. In the latter case the color was supposedly due to the oxidation of tyrosin to melanin, the tyrosin being formed in the breaking down of proteins when the carbohydrate supply was insufficient and unsuitable; but on the addition of zinc salts the color production was due probably not to the exhaustion of carbohydrate but to unfavorable conditions preventing its use.

The intense yellow water-soluble pigments diffusing into the medium is obviously a metabolic product, perhaps the chrysophanic acid of Zopf. In the case of the nitrate medium, at least, it might indicate unfavorable growth, although it doesn't especially appear so for all media, certainly not with glycerine agar.

#### D. POLARIZED LIGHT

Since, as has been stated, the walls of reproductive cells are sometimes of different constitution from vegetative cells and since they might possibly have peculiar physical characteristics, they were studied with a polarizing microscope. Agar-slide cultures and hanging drops were employed under high power and oil immersion. No structural differences were detectible by this method, although the twisted nature of the wall in the phialide was most conspicuously brought out. Sometimes, in ordinary mycelia, adjacent cells were noted to refract differently. This is presumably due to the different orientation of the cells caused by twisting, but it may have been that some of them were beginning to form chlamydo spores and hence were of different structure.

#### V. FUNGI IMPERFECTI AND SEXUALITY

Lindau's ('07-'10) treatment of the Hyphomycetes has been followed. The subfamily Cephalosporieae is separated from the Aspergilleae in that the spores are in balls in the former and in chains in the latter. The Aspergilleae include *Penicillium* and *Gliocladium*. *Clonostachys* belongs in the Verticillieae. *Allescheria Boydii*, also described in different develop-

mental stages as *Cephalosporium Boydii* and *Dendrostilbella Boydii*, because of its perithecial fructification, is placed in the Eurotiaceae of the Perisporiales. Clements and Shear ('31) have made *Allescheria* a synonym of *Eurotium*. The fertile state of *Gliocladium penicilloides* placed it in *Eurotium insigne* according to Winter ('87), but this disposition was later disputed by Matruchot ('95). Thom and some later workers have segregated the perfect forms of *Aspergillus*, as well as imperfect forms with similar conidia, in the Aspergillaceae, close to the Gymnoascaceae of the Plectascales.

#### A. EXPERIMENTS TO INDUCE SEXUAL FRUCTIFICATIONS

The author at first believed that the imperfect stages were merely labile and that perfect fructifications might possibly be produced by various special methods. In no case were these successful. After elaborate experimentation with a number of algae and other forms, Czurda ('33) came to the conclusion that copulation was caused only by pH and internal disposition, and since the latter was intangible, pH was the only factor subject to investigation. The present experiments did not indicate that there was a specific pH, at least one which was solely responsible. The usual media were employed to evoke fertile stages. Drying or maintaining at low temperatures merely showed the extreme longevity and resistance of these organisms. It was thought that by crossing nearly related species and varieties fertile stages might be attained. Therefore cross-inoculations were made of *Clonostachys Araucaria* and its varieties *rosea* and *confusa*, as well as of all of the species of *Cephalosporium*. The only noticeable result was an aversion of *Clonostachys Araucaria* and the variety *confusa*. The rest intermingled promiscuously. Agar micro cultures, as well as Petri plate specimens, were observed, and although no particular hyphal fusions were noted, neither were there ordinarily signs of repulsion.

#### B. INTERPRETATIONS REGARDING LOSS OF SEXUALITY

Ramsbottom ('33) believed that heterothallism and saltation were responsible for the origin of the Hyphomycetes.

Thus theoretically we may regard one of the Fungi Imperfecti as able to carry on the influence of the environment. If this is so it is possible that a permanent change may be brought about. . . . If such changes occur naturally then we may get differences which might throw heterothallism out of gear.

It was his suggestion that these should not be regarded as species but rather as form-species. Hansen and Smith ('32) held similar views on *Botrytis cinerea* which theoretically has a perfect stage in *Sclerotinia Fuckeliana*. They discussed previous explanations as (a) impure material, i. e., a complex of established types on the host which must be separated, (b) mutation, (c) hybridization, (d) microconidia—some possible significance but little evidence that they even have enough power of germination to play an important rôle, (e) anastomoses, hyphal fusions, heterocaryosis, i. e., condition of nucleus containing two or more genetically different nuclei, (f) mixochimaera (no cytological evidence of this yet). Their cytological studies showed that the mycelial cells and conidia were multinucleate. Further analyses of types were made by 128 single spore cultures, from which were selected 8 showing the greatest morphological variation. Twenty-five single spore cultures were made of these and a record kept for a number of generations. Hansen and Smith concluded that the regularity and completeness with which the homotypes separated from the heterotypes indicated that the character-determining elements were discrete units of limited number, suggestive that the basic unit of the individual was the nucleus and not the cell. Therefore a multinucleate spore, a colony really, cannot give rise to a genetically pure culture unless all of its nuclei are genetically identical. Gregory ('35) suggested the following explanation for loss of sexuality in the dermatophytes, namely, environmental factors, elimination of sexuality (negative adaptation to parasitism), and heterothallism.

Although the species here studied are uninucleate, heterothallism may well play a part. It is not unlikely that there are many races, new ones constantly being formed by the mechanism of hyphal anastomoses, and some of these are actually antagonistic although morphologically very similar. Perhaps some compatible strains have died out, leaving imperfect

halves to vegetate ceaselessly unless by saltations new harmonious ones shall arise.

## VI. MEDICAL ASPECTS

### A. PATHOGENICITY

Of the forms isolated from skin lesions—*Allescheria Boydii* and the species of *Cephalosporium*—there is some doubt as to real pathogenicity. Of the *Cephalosporium* species treated by Dodge ('35), only *C. Serrae*, of keratomycosis of the eye, and *C. Doukoureii*, of a gummatous lesion, are said to be pathogenic to laboratory animals.

*Allescheria Boydii*, isolated by Boyd and reported by Shear from a case of granular mycetoma of man, was thought by them to be a contaminant and not an anaerobic form because of its peculiar morphology within the foot and its inability to infect laboratory animals. A number of other Hyphomycetes, including species of *Indiella*, *Glenospora*, *Scedosporium*, *Aspergillus*, and *Penicillium*, have been reported as etiological agents of maduromycosis. At present it would seem that such were purely accidental contaminations, which may be fatal but are not naturally so.

The author secured species of *Penicillium* and *Aspergillus* frequently from eczematoid infections at the Barnard Free Skin and Cancer Hospital, and the *Cephalosporium symbioticum*, with the intimately associated *Torulopsis mucilaginosus*, from a particularly severe case of dermatomycosis. She also isolated the latter with a similar co-form which was eliminated in subsequent dilution cultures from a case of pemphigus vulgaris. Apparently the same red yeast was found by Engelhardt ('27) in a case of pemphigus. He illustrated the organism as it grew in the host, i. e., filamentously, similar to the condition here found on nitrate agar, although no cephalosporia were shown. Whether such organisms are purely saprophytic secondary or primary invaders, or necessary symbionts of forms better believed to be pathogenic (Hartmann, '26), in the present case of a *Cephalosporium* and *Torulopsis mucilaginosus*, is as yet unknown; but immediate evidence at

least indicates that they have rather specialized habitats, and constitute a group which should be investigated from a pathogenic viewpoint.

The various species of *Cephalosporium* have been regarded as accessory perhaps symbiotic saprophytes. Hartmann ('26) found *C. niveolanosum* associated with *Trichophyton gypseum* and left the question open. So great a number have been secured from superficial lesions that although animal inoculations may be negative (perhaps due to methods of inoculation) a parasitic nature is certainly suggested. The author has found species of *Cephalosporium* from superficial lesions of the glabrous skin especially. Various species of *Penicillium* and *Aspergillus* are even more common. *Alternaria*, *Sarcina lutea*, and *Torulopsis mucilaginosus* are likewise frequently found. Some species of *Cephalosporium* are also reported as saprophytic in nature on soil or humus. None of these were studied; but an organism treated by Buchanan ('11) as *Cephalosporium Pammelii* appears different from the skin group, at least in the possession of multiseptate conidia, whereas only uniseptate ones are found in the group here investigated. Species of *Cephalosporium* have also been found on insects (Petch, '28) and as causative agents in various plant diseases. In the Dutch elm disease it is only a stage of an organism, of which the perfect stage is *Ceratostomella Ulmi* of the Sphaeriales. Reddy and Holbert ('24) gave a good description of the effects of *C. Acremonium* Corda emended Fresenius, upon corn, causing the black bundle disease. In all these cases it is the transporting system which is attacked. The habitat would certainly indicate parasitic tendencies which might as well be developed in animal tissues as in those of the plant.

#### B. OCCURRENCE OF GRANULES IN CULTURE

One strange cultural condition certainly deserves further mention. On blood serum *C. rubrobrunneum*, after several weeks, produced numerous small white spherical bodies several mm. in diameter. Under low power they appeared surrounded by a fine felt of white to pale pink mycelium (pl. 6, figs. 15-16). These proved to be very hard and when crushed revealed a



white chalky interior. Under higher power numerous linear crystals radially arranged were seen. These crystals did not stain with lacto-phenol and cotton blue, nor with glycerine-eosin, and there was no definite cellular mass visible, although there were some irregularly shaped stainable masses. The latter were suggestive of the granular bodies occurring sometimes in the animal body, in fact quite definitely characteristic of certain diseases. Of late such have been noted more frequently upon artificial culture (Area Leão and Lobo, '34).

Two recent papers (Almeida, '34, and Weidman, '32) gave rather fully the history of granular occurrences. These varied in the host from the capsules of bacteria, *Saccharomyces hominis* and *Cryptococcus histolyticus*, to the radiating structures of purely membranal or cellular nature, as in *Aspergillus*, and the definite extra-cellular grains produced in *Actinomyces*, Madura foot, and the like. They have been interpreted as a reaction to the host comparable to distortions of haustoria, as living structures capable of absorbing food, etc., or as mere dead extensions of the membrane. They are compared to the "Hülle" cells first mentioned by Eidam ('83) in species of *Aspergillus*—all strains of the *A. nidulans* group and some strains of *A. terreus*, *A. flavipes*, and *A. ustus*. These cells develop from older mycelia as smaller branches, and the terminal and subterminal cells become surrounded by a very thick mucilaginous wall, comparable to that of *Saccharomyces hominis* produced in the host. The other structures have been evoked upon organic media frequently—a fact which eliminates a vital cause and probably puts such formations on a chemical basis. Weidman ('32) compared these incrustations to the similar mechanism in the "Dauercyst" of protozoa, i. e., that the capsule (especially) is protective against adversity and preparatory to reproduction, as likewise the asci in fungi are reproductive cells whose development is stimulated by unfavorable conditions. He does soften this rather far-fetched homology of reproduction and adverse conditions (although such was probably the primitive state) by saying that possibly reproduction could be absolutely separated from environmental factors. He thought that adverse conditions might also be assumed for

fungi in the comparatively anaerobic and warm environment of the mammalian tissue.

Incrustations of the type found by the author are extramatrix, of the "calcareous incrusting substance" type in Weidman's classification. Their origin and purpose are poorly comprehended, but they are probably reminiscent of pathological conditions in the host. Various solvents (concentrated acids of sulphuric, nitric, and hydrochloric) were tried on these crystalline masses which it was conjectured might be calcium oxalate. The most rapid action occurred in hydrochloric acid, releasing numerous square-oblong flat crystals and some loose cubical arrangements of about sixteen small ones; and the remainder of the ball appeared segmented with fine long crystals which protruded radially. In nitric acid there was much bubbling, and the balls assumed a rougher appearance under the microscope but dissolution was very slow. The bubbles were colorless, of a peculiar hexagonal outline, and their heavy part contained small crystalline fragments. In sulphuric acid there were crystals similar to those in the hydrochloric acid, and some hollow ones. It could not be noted if the ball were actually diminishing in mass, but the liquid around it seemed of a deeper yellow than the normal acid, perhaps indicating solution.

## VII. TAXONOMY AND MORPHOLOGY

The general classification of this group has been given in a previous section, and only the individual members will be discussed here. Due to the temporary nature of this group, much changing of nomenclature is both unnecessary and confusing. A couple of very obvious errors are corrected, however, i. e., in regard to the former *Gliocladium roseum* and *Clonostachys spectabilis*. The new organism isolated by the author is described as *Cephalosporium symbioticum*. Descriptions are based mainly upon giant colonies grown upon glycerine agar. The names of the colors are according to Ridgway ('12).

*ALLESCHERIA* Sacc. & Syd. in Sacc. Syll. Fung. 14: 464. 1899.

It was thought that if this form were included with a known

fertile stage more light might be shed upon the significance of the conidiophore. Unfortunately, the entire life cycle was not recalled and a complete cytological study was impossible. The conidiophores are poorly developed and resemble somewhat those of *Cephalosporium*; but the dimorphism of conidia is a constant feature, and the soft downy colony is quite distinct from the smooth rope-like one of *Cephalosporium*; so that it is doubtful if even the spore-ball stage should be included in that genus. Type: *Eurotiopsis Gayoni* Costantin.

1. *ALLESCHERIA BOYDII* Shear apud Boyd and Crutchfield, Am. Jour. Trop. Med. 1: 258-268. 1921; Mycologia 14: 239-243. 1922. Pl. 1, figs. 18-28.

Colony: pale gray velvety, of short filaments, sometimes becoming greenish in spots, or with much longer pile and approaching white, cerebriform and growing into medium at edges; reverse slightly hardened and wrinkled; growth relatively slow.

Conidiophores: simple; phialides on aerial mycelia, 3-20  $\mu$  long, septate or not, cutting off oblong conidia which adhere irregularly; spores with two oil droplets, ovoid, capable of immediate germination,  $8 \times 5.5 \mu$ , heavy-walled spores occasionally preceding hyaline ones, the former characteristic of single-spored phialides of coremia,  $15.5 \times 4 \mu$ ; terminal chlamydospores  $8.5 \times 11 \mu$ .

Habitat: isolated from a case of granular mycetoma in a negro. Culture of Shear, from Baarn.

*CEPHALOSPORIUM* Corda, Icon. Fung. 3: 11. 1839.

Colony: smooth, much corrugated, rope-like, forming a consistent layer, slightly adherent.

Conidiophores: simple or with few short lateral branches along cords of hyphae; hyphae repent, phialides long and slender, only slightly narrower at tips than at base, bearing spores in slime balls; coremia frequent on certain media; chlamydospores present. Type: *C. Acremonium* Corda.

The six species here studied form quite a homogenous group. *Cephalosporium symbioticum* and *C. Serrae* vary most widely,

the former including yeast-like growth and becoming fuscous with chlamydospores, the latter becoming pubescent and also dark with chlamydospores.

#### KEY TO SPECIES OF CEPHALOSPORIUM

1. Producing some yeast-like growth on solid culture, apricot-buff, becoming fuscous ..... *C. symbioticum*
1. Not found to produce yeast-like growth in culture..... 2
2. Colony white with a rough dry surface, eventually becoming fuscous due to chlamydospores..... *C. Serrae*
2. Colony not becoming fuscous..... 3
3. Colony moist, rope-like, turbinate..... 4
3. Colony dry, often with a bloom, irregularly dissected..... 5
4. Colony ivory to pale pink; conidiophores simple; spores  $6 \times 3 \mu$ ..... *C. niveolanosum*
4. Colony soon becoming deep orange; conidiophores simple or branched; spores  $2-4 \times 1.5 \mu$ ..... *C. kiliense*
5. Surface of colony smooth, cerebriform, seashell pink; spores  $7 \times 1.5 \mu$ ..... *C. rubrobrunneum*
5. Surface of colony short-pubescent, slightly convolute, white to salmon-buff; spores  $4-5.5 \times 2.5-3 \mu$ ..... *C. Stuehmeri*

1. CEPHALOSPORIUM RUBROBRUNNEUM Nannizzi, Tratt. Micopat. Umana [Pollacci] 4: 455. 1934. Pl. 2, figs. 22-25.

*C. rubrobrunneum cerebriforme Hartmanni* Benedek, Arch. f. Derm. & Syphilis 154: 166. 1928.

Colony: at first an irregular small dry pink heap in center, spreading irregularly for about a cm., then flat, about 1 mm. thick, moderately dry, whitish pubescent at edges, center of coremia becoming frosted, seashell pink, very cerebriform, edges abrupt; little guttational water; reverse corrugated and consistent, pale orange, little color diffusing into medium; no coremial balls.

Conidiophores: borne on ropes of numerous hyphae up to  $11 \mu$  in diam., surrounded by thick mucus, spreading from both sides, non-septate, up to  $30 \times 2-3 \mu$ , producing spores in balls  $5-15 \mu$  in diam., or irregularly clinging along sides of phialides in packets; spores oblong-ellipsoid,  $7 \times 1.5 \mu$ , or almost spherical,  $2-2.5 \mu$ , sometimes slipping past each other at only a slight angle and forming a column; terminal chlamydospores on wort agar,  $17 \times 14 \mu$ , globular crystalline bodies on serum (see pl. 6, fig. 9, and discussion p. 35).

Habitat: isolated from a case of dermatitis in Frankfort, a.M., Germany. Culture of Pollacci, from Baarn.

2. *CEPHALOSPORIUM STUEHMERI* Schmidt & Beyma in Beyma, Centralbl. f. Bakt. I, 130: 102-105, 3 figs. 1933.

Pl. 2, figs. 17-21.

Colony: white to a pale pink, slightly pubescent above, little aerial growth, small white balls 1 to several mm. in diam. arising on elevated spots of colony in cultures 7-10 days old, about as thick as heavy paper; guttational water; reverse corrugated, pale orange, as is also adjacent medium; small coremia on Sabouraud's medium, and on carrot plugs a white pustular tallowy growth.

Conidiophores: unbranched, usually one to several septate, borne in a row along both sides of a straight hypha; sheaths of hyphae often with some strands protruding and bearing spores; phialides  $35 \times 1.5 \mu$ ; cephalosporia  $10-15 \mu$ ; conidia ellipsoid,  $4-5.5 \times 2.5-3 \mu$ , swelling slightly on germination, sprouting at one point and giving a mycelium that becomes early septate; vegetative cells  $10 \times 2 \mu$ , uninucleate; submerged terminal chlamydospores  $6.5-7 \mu$  in diam., intercalary ones  $7 \mu$ .

Habitat: eczematoid infection of skin, Germany. Culture of Stuehmer, Baarn.

3. *CEPHALOSPORIUM KILIENSE*<sup>3</sup> (Gruetz) Hartmann, Derm. Woch. 82: 569. 1926.

Pl. 2, figs. 26-31.

*Acremonium kiliense* Gruetz, Derm. Woch. 80: 765-774. 1925.

*C. asteroides griseum Gruetzii* Benedek, Arch. f. Derm. & Syphilis 154: 166. 1928.

*C. Acremonium* Pollacci & Nannizzi, I Miceti Pat. Uomo Anim. 9: No. 81. 1930. Non Corda, 1839.

Colony: a few mm. thick, bittersweet-orange, finely corrugated, consisting of a number of small irregularly arranged strands, aerial growth slight, flat, and parallel; mycelium extending up on glass and consisting mainly of relatively thick cords upon which tiny cephalosporia can be seen with a lens;

<sup>3</sup> See Dodge, Med. Myc. p. 828. 1935.

much guttational water; reverse slightly irregular, lighter-colored than upper surface; on Sabouraud's dextrose agar a faint white surface powder; on carrot plug an orange hairy coremial growth.

Conidiophores: along both sides of main stalk, especially clustered at ends and upon lateral branches where compound phialides are often borne in whorls of four or more, forming cephalosporia up to  $14\ \mu$  in diam. in the air, or irregular non-slimy packets; phialides slightly tapering,  $2-43 \times 2.5\ \mu$ ; conidia oblong-ellipsoid, hyaline,  $2-4 \times 1.5\ \mu$ ; terminal chlamydospores  $4-7 \times 2-5\ \mu$ , intercalary ones  $5\ \mu$  in diam.

Habitat: gummata and ulcers in man. Culture of Pollacci (?), from Baarn.

4. *CEPHALOSPORIUM SERRAE* Maffei, Atti Ist. Bot. R. Univ. Pavia IV, 1: 183-198, 9 figs. 1930. Pl. 2, figs. 1-11.

Colony: about 5 mm. thick, corrugated, at first white then sea-shell pink, in about ten days turning fuscous, aerial growth rough and coarse wooly, of short projections several mm. high, heaped, dry and partially wrinkled; a bit of fine growth on glass; no guttational water; reverse wrinkled and black; no color diffusing into medium; on carrot plug an olive-buff pustular glabrous growth with a few pink coremia.

Conidiophores: borne laterally, simple or once-seriate, of 3-5 phialides; main stalk  $42\ \mu$  long; phialides somewhat tapering,  $29 \times 2.5\ \mu$ ; cephalosporia  $7.5\ \mu$  in diam.; conidia ellipsoid,  $3-4 \times 1.5\ \mu$ , sometimes not in a ball; chlamydospores  $7.5 \times 5\ \mu$  and  $10 \times 3.5\ \mu$ , terminally or on strands of upright coremia.

Habitat: keratomycosis of the eye. Culture of Pollacci, from Baarn.

5. *CEPHALOSPORIUM NIVEOLANOSUM* Benedek, Arch. f. Derm. & Syphilis 154: 166. 1928. Pl. 2, figs. 12-16.

Colony: at first elevated, ivory-white, pasty, 5 mm. in diam., becoming a slightly pink, glistening, dry heap, edges flat with radial striations arranged turbinately (in the dark remaining ivory-white but becoming pink upon exposure to daylight); short delicate coremia at times; reverse convex from medium.

Conidiophores: simple, rare, septate or not; spores ellipsoid with two oil droplets,  $6 \times 3 \mu$ ; hyphal cells  $20 \times 2.5 \mu$ ; intercalary submerged chlamydospores  $6.5 \mu$  in diam., terminal thinner-walled ones,  $15 \mu$ .

Habitat: isolated from a case of dermatitis in Leipzig. Culture of Benedek, from Baarn.

6. *CEPHALOSPORIUM symbioticum*<sup>4</sup> Pinkerton, n. sp.

Pl. 2, figs. 32-38, 45-46.

Colony: apricot-buff, on wort agar sometimes becoming drab-green, with smooth surface except for small coremia, convoluted, growing into medium below; on liquid media producing a ring or pellicle, decolorizing litmus, coagulating milk, liquefying gelatine, no gas in sugars, producing acid in dextrose, d-levulose, raffinose, maltose, and sucrose, alkali in amygdalin, arabinose, d-galactose, lactose, and dextrin.

Within medium colony forms pseudomycelium of cells  $4.0 \times 2.5 \mu$ , cephalosporia  $8 \mu$  in diam. at the apex of phialides, the latter  $5 \mu$  in length; aerial thallus a true mycelium, cells  $8-10 \times 2 \mu$ ; phialides  $2-5 \mu$  in diam.; spores  $4-5 \times 2.5 \mu$ , some germinating in place. Mature colonies becoming fuscous with many terminal and intercalary chlamydospores  $4-5 \mu$  in diam.

Habitat: isolated from a severe case of dermatitis at the Barnard Free Skin and Cancer Hospital. It was intimately associated with *Torulopsis mucilaginoso* from which it was separated only by extreme dilution cultures. The subgenus *Cephaloblaston* of Ciferri ('32), typified by *C. pseudofermentum*, would also encompass this species.

<sup>4</sup> *CEPHALOSPORIUM symbioticum*, sp. nov.

Colonia: "apricot-buff" aliquando "drab-green," in medio musto, superficiei laevi praeter coremia parvo, convoluta, in media subter succrescens; in mediis liquidis annulum pelliculumve efficiens, litmo decolorans, lactem coagulans, gelatinam liquefaciens, in saccharis non effervescans; acidum in "dextrose, d-levulose, raffinose, maltose, sucrose" faciens, alcalinum in "amygdalin, arabinose, d-galactose, lactose, dextrin."

Colonia mycelium falsum intra medium formans, cellulis  $4.0 \times 2.5 \mu$ , cephalosporiis  $8 \mu$  in diametro apice phialae  $5 \mu$  in longitudine; thallus aerius mycelium verum, cellulis  $8-10 \times 2 \mu$ ; phialae  $2-5 \mu$  in diametro; sporae  $4-5 \times 2.5 \mu$ , aliquibus in situ germinantibus. In coloniis maturis fusciscentibus chlamydosporae multae terminales aut intercalares,  $4-5 \mu$  in diametro.

*Case History.*—The patient, a white female 15 years of age, first reported to the Barnard Free Skin and Cancer Hospital on April 2, 1934. She had a severe dermatitic eruption occurring in patches upon her hands, especially the fingers, and upon the forearms. The case was diagnosed as "dermatitis contact." Trichophyten tests were given and crude coal-tar salves advised. Various patent medicines previously used by the patient complicated the irritation. By August 31, 1934, there was a marked improvement, but on September 20, the condition was worse and X-ray treatments were given. On October 2, the hands showed many new vesicles and bullae and ruptured blisters which left raw spots. The condition was then diagnosed as a combination of tinea and *Staphylococcus* infection. She also suffered from acne and reported a history of scabies. In addition to X-ray treatments, a tincture of xeroform was recommended. The patient was last heard from on October 24, 1934.

Skin cultures included numerous organisms of which *Staphylococcus*, *Torulopsis mucilaginosus*, *Cephalosporium symbioticum*, and a black filamentous form (unidentified) were dominant. The *Cephalosporium* was non-pathogenic to white mice.

CLONOSTACHYS<sup>5</sup> Corda, Pracht-Flora, p. 31. 1839.

Creeping hyphae; conidiophores simple or branched; phialides four or more branched, verticillate; spores adhering in cephalosporia. Type: *C. Araucaria* Corda.

1. CLONOSTACHYS ARAUCARIA Corda, Pracht-Flora, p. 31. 1839. Pl. 5, figs. 14–26.

Colony: white-cottony, soon turning pale flesh to seashell pink, powdery, rapidly growing; coarse white-pink coremia in older cultures; mycelium extending up glass for several mm., bearing cephalosporia; much guttational water; reverse wrinkled. Species differs superficially from the former *Gliocladium roseum* in pinker color, slower growth, less extensive coremia formation, and producing acid in maltose.

Conidiophores: polymorphic, some of the characteristic of four-branched type; asymmetrical penicillate fructifications

<sup>5</sup> The investigation of the type species and varieties permits enlargement upon Corda's original limited description. Unfortunately, the author is unfamiliar with the other species usually included here, but because of the limited generic description it is doubtful if they form a homogeneous group. The type, which has been inadequately characterized, does seem sufficiently different to justify its position in a genus intermediate between *Cephalosporium* and *Gliocladium*. *Clonostachys spectabilis*, which was studied only briefly due to an early demise, obviously is far removed and certainly suggests *Botrytis*. Presumably Oudemans ('86) compared the botryoid spores to the lateral protrusions sometimes found on *C. Araucaria* and its varieties, which are not spores.



formed on reversed wort plates with terminal clusters of six phialides and laterals of three to six, phialides  $10 \times 2 \mu$ , flask-shaped and bent outwards, conidia spherical to ellipsoid,  $3 \times 1-2 \mu$ ; cephalosporia borne along the main cord, singly or in clusters of three to six, phialides slightly flask-shaped,  $17-33 \times 1.5-4 \mu$ ; cephalosporia  $13 \mu$ , conidia  $5.5-6.5 \times 2.5-3 \mu$ ; hyphae warty, especially near cephalosporia; chlamydospores rare, on corn meal agar in terminal series,  $13 \times 10 \mu$ ; or on lactose broth intercalary,  $10 \times 12.5 \mu$ ; hyphal cells  $13 \times 3 \mu$ .

Habitat: "In cortice ramulorum arborum in Germania, Brittainia" (Corda). Culture of Wakefield, from Baarn.

2. *CLONOSTACHYS ARAUCARIA* var. *ROSEA* Preuss, *Linnaea* 25: 727. 1852. Pl. 4, figs. 27-31.

Colony: salmon-pink almost at first, mottled with white, floccose, of strands several mm. long, heaped in center and irregularly wrinkled, coarsely flocculent at edges; much guttational water; reverse wrinkled. Variety differs from the former *Gliocladium roseum* and the species in the salmon tint, intermediate speed of growth, and is more wrinkled than either.

Conidiophores: mostly typical of four phialides as illustrated by Corda, the spores from several phialides sometimes forming confluent slime balls; cephalophores up to  $100 \mu$ ; phialides non-septate,  $17-40 \times 6 \mu$ ; cephalosporia  $21 \mu$  in diam.; conidia  $4 \times 5 \mu$ ; chlamydospores terminal and intercalary,  $3.5 \times 10 \mu$ .

Habitat: "In ramulis, in piris et pomis immaturis dejectis, frequens, Hoyerswerda" (Preuss). Culture of Shapovalov, from Baarn.

3. *CLONOSTACHYS ARAUCARIA* var. *confusa* Pinkerton, n. var. Pl. 4, figs. 15-26.

*Penicillium roseum* Link (?), *Ges. Naturforsch. Fr. Berlin*, Mag. 7: 37. 1816.

*Gliocladium roseum* Bainier, *Bull. Soc. Myc. France* 23: 111-112, pl. XV, figs. 1-6. 1907. Nec *Clonostachys Araucaria* var. *rosea* Preuss.

Colony: pale ochraceous salmon, slightly mottled with

white, short-cottony and mealy on top, growing up tube very little, slightly adherent; on inverted Petri plate of wort agar producing white feathery extensions measuring up to 1 cm. long; much guttational water; reverse much wrinkled.

Conidiophores: polymorphic; penicillate conidiophores asymmetrical with branches terminating in whorls of three to four, penicillus  $85\ \mu$  high, main lateral segments  $45\ \mu$ , phialides  $8-10 \times 1.5-2\ \mu$ , flask-shaped, mature conidia spherical to slightly falcate,  $5\ \mu$ , swelling on germination to  $8-10\ \mu$ , growing from one or both poles; spore balls from single phialide along main hyphae or rope, or usually in whorls of three, borne laterally or terminally, phialides  $30-40 \times 3-4\ \mu$ , warty, straight or slightly narrower at top, adjacent balls sometimes becoming confluent and reaching  $10-30\ \mu$  in diam., conidia ellipsoid, smooth, hyaline, pink in mass,  $6-7 \times 4-5.5\ \mu$ ; chlamydospores rarely formed but found terminally on submerged hyphae on Raulin's agar,  $4.5\ \mu$  in diam., also on inverted wort plates, intercalary ones  $14 \times 20\ \mu$ .

Habitat: "In caule solani tuberosi exsiccati. Misit Dr. Nees ab Esenbeck." (Link); "du carton pourri" (Bainier). Culture from Thom No. 454-4640.428, from Kral in Prague, Bohemia.

Bainier stated that this form resembled *Acrostalagmus roseus* of the Verticillieae except that the precedence of penicillate over verticillate series was reversed in *Gliocladium*. More probably the variations are dependent upon nutrient relations, especially moisture conditions. On lactose broth hanging drops, the spore balls are most luxuriant, as are also the warts. Complex penicillate fructifications are also present, however, and in fact precede the simpler cephalosporial stage both in time and on the main trunk. The spores on the penicillus cling together only loosely in irregular chains as seen on slide cultures, and are quickly disseminated in water. Conspicuous deliquescence of the penicillate heads, as occurs in *G. deliquescens*, was not noted. The fact that in crossing this form is antagonistic to the species, whereas the rest are all indifferent, might indicate a close relationship of a lethal nature.

4. *CLONOSTACHYS SPECTABILIS* (Harz) Oudem. & Sacc. Ned. Kruidk. Arch. II, 4: 539. 1886. Pl. 5, figs. 1-7.

*Botrytis spectabilis* Harz, Bull. Soc. Imp. Nat. Moscow 44: 88-147. 1871.

Original colony gray-white and fuzzy, turning black due to production of numerous conidia.

Conidiophores compound, dichotomously branched and bearing spores on short stalks laterally along the phialides; spores spherical, 6.5-7  $\mu$  in diam.; chlamydospores 6.5-10  $\mu$  in diam.

Habitat: "sur la tannée dans les serres du jardin botanique d'Amsterdam" (Balen). Culture of Shear, from Baarn.

*GLIOCLADIUM*<sup>6</sup> Corda, Icon. Fung. 4: 30-31. 1840.

Conidiophores erect, septate, penicillately branching above, branches and branchlets septate, appressed, forming a solitary gelatinous head; conidia unicellular, borne upon the tips of branchlets and held together by mucilaginous substance in a dense mass, those on adjacent phialides fusing. Type: *G. penicilloides* Corda.

1. *GLIOCLADIUM FIMBRIATUM* Gilman & Abbott, Iowa State Coll. Jour. Sci. 1: 304, fig. 38. 1927. Pl. 3, figs. 33-41.

Colony: at first white, fuzzy, nearly circular, very thin, moist, translucent with parallel wrinkles, finally antique green, mottled with white, dry, floccose, faintly zonate and radially striate, broad masses of white hyphae growing up tube several cm.; reverse radially corrugate.

\* The inclusion of the former *Gliocladium roseum* in *Clonostachys* might possibly also justify lumping *Gliocladium* in that genus whose publication preceded it by one year. However, the three sections of *Gliocladium* mentioned by Thom ('30)—the rose, white, and green series—seem quite distinct culturally and morphologically. There is one common character to the two genera, i. e., the lack of disjunctors and presence of cephalosporia, which in view of the heterogenous mass included under *Penicillium* might make such a segregation logical.

*Gliocladium penicilloides* resembles *Clonostachys Araucaria* in a rather similar zonate growth and exudation of yellow color into medium, but differs in the thin-walled auxiliary cells (akinetes). *G. Vermoeseni* is quite distinct in its colonial characters and the spore type which approaches *Penicillium* in its rigidity, but still lacks disjunctors. *G. deliquescens* and *G. fimbriatum* are very different from each other as well as the others in colonial characters but have akinetes. Therefore, due to insufficient knowledge of the *Gliocladium* and *Clonostachys* segregates as a whole, they will not be combined here.

Conidiophores: homogeneous, borne laterally and terminally in a wide range of heights up to  $300\ \mu$ , more or less symmetrical in two series, basal cell  $14.5 \times 5.3\ \mu$ ; first series  $6.5 \times 4\ \mu$ ; phialides very turgid and asymmetrically flask-shaped,  $8.5 \times 4.5\ \mu$ ; spores ellipsoid,  $4.5 \times 3.3\ \mu$ , forming irregular spore balls up to  $16.5\ \mu$  in diameter, dry and only slightly mucoid; akinetes terminal and intercalary, frequent,  $11-13 \times 8.5-10\ \mu$ , containing oil droplets up to  $1.3\ \mu$ , these soluble in chloroform leaving striations; chlamydospores intercalary,  $9-9.5 \times 8\ \mu$ .

Habitat: in soil, Iowa and Louisiana. Culture of Gilman & Abbott, from Thom No. 459-4894.20.

2. *GLIOCLADIUM DELIQUESCENS* Sopp, Monogr. pp. 89-93, *taf. I, fig. 1-6*. 1912. Pl. 3, figs. 20-32.

Colony: at first colorless, of mainly submerged hyphae, quickly becoming thin and white-floccose over whole surface, then meadow-green and slimy, progressing slowly centripetally from edge; much guttational water; very rapid growth of hyaline semi-submerged radiating hyphae.

Conidiophores: of two types—penicillate and simple cephalosporial; penicilli at first white but spores become green and aggregate in a heavy slime, typically tri-seriate and each series trichotomous; brush  $45 \times 40\ \mu$ ; first series  $17.5-24 \times 4\ \mu$ ; second series  $9-11 \times 4\ \mu$ ; phialides  $6-9 \times 2-2.5\ \mu$ , spores smooth, spherical to ellipsoid,  $3.5 \times 2.5\ \mu$ , germinating spores swelling up to  $6.5-9\ \mu$ , sprouting in one or more places; spore balls up to  $30\ \mu$ ; cephalosporia up to  $60\ \mu$ , circular with thick matrix of slime, cephalolides  $40 \times 6\ \mu$ ; conidia  $2\ \mu$  in diam.; akinetes  $7.5-10 \times 6.5-8.5\ \mu$ , terminal or intercalary; pseudoterminal ovoid cells  $14 \times 11.5\ \mu$ ; chlamydospores  $6 \times 7.5\ \mu$ .

Habitat: on *Daedalea unicolor* in Norway. Culture of Thom No. 457-4894.17.

3. *GLIOCLADIUM VERMOESENII* (Biourge) Thom, *The Penicillia*, p. 502. 1930. Pl. 4, figs. 1-14.

*Penicillium Vermoesenii* Biourge, *La Cellule* 33: 230. 1923.

Colony: pale vinaceous, rapidly growing, irregularly powdery and with thin long hairs; much guttational water; reverse homogeneous and when viewed through appears splotchy.

Conidiophores: usually penicillate,  $45\ \mu$  long from first branch, decidedly asymmetric, poly-seriate, final series trichotomous; phialides up to  $10 \times 1.5\text{--}3.5\ \mu$ ; spores spherical,  $2.5\ \mu$ ; cephalolides  $40\ \mu$  and more, cephalosporia  $20\text{--}25\ \mu$ , cephalospores ellipsoid,  $5\text{--}6.5 \times 4\ \mu$ ; intercalary chlamydospores  $13 \times 15.5\ \mu$ , terminal  $5 \times 11\ \mu$ ; akinetes  $15\ \mu$  in diam.; arthrospores  $10.5 \times 5\ \mu$ ; oidia  $3 \times 5.5\ \mu$ , rare.

Habitat: parasitic or semi-parasitic on certain species of *Areca*. Culture of Westerdijk, from Thom No. 451-5090.4a.

4. *GLIOCLADIUM PENICILLOIDES*<sup>7</sup> Corda, Icon. Fung. 4: 31, taf. 7. figs. 88-89. 1840. Pl. 3, figs. 1-19.

Colony: at first chalky-white, of short regularly centrifugally appressed hairs, faintly and scarcely striate, within a month very dry and tan to light pink. On glycerine agar sometimes producing a lemon-yellow pigment which diffuses into the medium; growth relatively slow and consistent.

Conidiophores: asymmetric, often borne as more or less short laterals along main branch, up to  $114\ \mu$  long, septate; phialides  $17 \times 3\ \mu$ , slightly flask-shaped, borne in threes, occasionally fours or more, of which one is larger; lowest branches alternate, usually not more than three main divisions; spores ellipsoid,  $5.5\text{--}6.5 \times 3\ \mu$ , swelling before germination to  $8 \times 5\ \mu$ ; single branched phialides, septate or not,  $35.5 \times 2.5\ \mu$ , bearing cephalosporia  $14\ \mu$  in diam.; spores  $4 \times 2.5\ \mu$ ; vegetative cells  $3.5\text{--}5\ \mu$  in diam., racquet-shaped, consisting of several large vacuoles; akinetes  $10\ \mu$  in diam., full of oily reserves and capable of almost immediate germination.

Habitat: on rotting *Thelephora*. Culture of Thom No. 453-5113.

*SCOPULABIOPSIS* Bainier, Bull. Soc. Myc. France 23: 98. 1907.

Type: *Penicillium brevicaulis* Saccardo.

<sup>7</sup> Winter ('87) suggested that probably *Eurotium insigne* Winter was the ascosporic form of this species. Matruchot ('95) found perithecia of the *Plectascales* type, but through the unique method of ascospore germination distinguished it from *E. insigne*; however, he offered no other nomenclatorial suggestion. Theoretically, the species should be removed to the perfect classification, but for the present such shall not be attempted.

1. *SCOPULARIOPSIS BREVICAULIS* (Sacc.) Bainier, Bull. Soc. Myc. France **23**: 99–103, pl. 11, figs. 1–6. 1907. Pl. 5, figs. 8–13.

*Penicillium brevicaule* Sacc. Fung. Ital. taf. 893. 1881.

White flocculent growth upon glycerine agar.

Conidiophores simple or few-branched; phialides  $8 \times 2-3 \mu$ ; spores  $5 \mu$  in diam. with disjunctors between, adhering in chains indefinitely; no mucus; no chlamydospores noted.

Habitat: one strain reported as pathogenic by Dr. D. J. Davis of Chicago. Culture of Thom No. 4858.

This species was studied only very superficially as living material, in an attempt to correlate the presence of disjunctors and no slime with the lack of disjunctors and mucus, also to note methods of phialide mechanism.

*TORULOPSIS* Berlese, Giorn. Viticoltura ed Enologia p. 54. 1894.

Type: *T. rosea* Berlese.

*TORULOPSIS MUCILAGINOSA* (Jørgensen) Ciferri & Redaelli, Atti Bot. Ist. R. Univ. Pavia III, 2: 256. 1925.

Pl. 2, figs. 39–44, 47.

*Torula mucilaginosa* Jørgensen, Die Mikroorg. d. Gärungsindustrie. ed. 5, 402. 1909.

*Rhodotorula mucilaginosa* Harrison, Trans. Roy. Soc. Canada **22**: 187. 1928.

*Cryptococcus rubrorugosus* Castellani, Arch. of Derm. & Syphilol. **16**: 403. 1927.

*Rhodotorula mucilaginosa* race *rubrorugosa* Lodder, Anaskosporogenen Hefen **1**: 104–105. 1934.

Colony: Carnelian red to scarlet, moist and smooth, pasty, rapidly growing upon wort and maltose agar, with elliptical cells showing bipolar budding and a pair of oil droplets in mature cells; on nitrate medium, following the sparse red surface growth, a submerged irregular hyaline one of pseudomycelial cells and small asymmetrical cephalosporia up to  $15 \mu$  sometimes occurring, spores  $2.5 \times 5 \mu$ ; in malt broth a ring, some red basal proliferation and slight pseudomycelial growth throughout liquid; slight growth in ethyl alcohol; ring in grape juice but no fermentation, no liquefaction of gelatin, milk clotted; no

gas in sugar solutions; acid produced in sucrose, d-levulose, maltose and dextrose, alkali in arabinose, amygdalin, d-galactose, lactose, raffinose and dextrin.

Habitat: originally isolated as a laboratory contaminant; Castellani reported it from scrapings in the axilla; and it was secured by the author from skin scrapings in a severe dermatomycosis.

### VIII. SUMMARY

1. The term cephalophore has been applied to a conidial fructification wherein the spores are held in a spherical mass by mucilage. These spores are found to be produced endogenously by cleavage following exudation of liquid which forms the matrix of the spore ball. Terminal granules seem to be kinetic centers associated with exudation and spore discharge. The phialides are thought to be uninucleate as are also the spores.

2. Accessory spore forms include chlamydospores in all cases, associated both with the aerial and submerged mycelium, oidia infrequently, and thin-walled spores in some, which have been called akinetes after the algological terminology.

3. An attempt has been made to correlate comparative cultural data regarding color, macroscopic and microscopic characters. It is believed that such factors as hydrogen-ion concentration, surface tension, oxygenation, and the nature of the nutrients are especially important in producing favorable or unfavorable conditions for the organism. Good growth is characterized by abundance of aerial mycelia with a considerable pigmentation; and poor growth, by numerous spore-forms, attenuated aerial hyphae with proportionally more reproductive bodies and a tendency towards submerged growth and exudation of pigments into the medium, and a paler color of the organism. *Torulopsis mucilaginos*a develops a pseudomycelium in the submerged state and loses its red color.

4. Mycelial pigmentation is noted in some cases to be more intense under optimal conditions; in some to be light labile. The solubilities of the pigment of *Cephalosporium kiliense* are listed, although no identification is made.

5. Polarized light indicates no structural difference between the walls of the phialides and of the mycelial cells.

6. Various unsuccessful attempts have been made to produce sexual fructifications. Theories regarding loss of sexuality are discussed, but no further contributions are suggested.

7. The clinical findings of some of the organisms in dermatomycoses are mentioned, although their pathogenicity has not been proven. The granular incrustations upon serum are described. These were found to be composed of fine needle-like crystals arranged radially and including no recognizable organic matrix but surrounded by fine mycelial filaments. The crystals were slowly soluble in the concentrated heavy acids. The theoretical significances of these structures are discussed.

8. A brief morphological description is given of all the forms studied. *Gliocladium roseum* (Link?) Bainier is described as *Clonostachys Araucaria* var. *confusa*. The position of *Gliocladium penicilloides* is discussed. The new species isolated from the dermatomycosis case at the Barnard Free Skin and Cancer Hospital is designated as *Cephalosporium symbioticum*.

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## EXPLANATION OF PLATE

## PLATE 1

All drawings, except fig. 17, made with the aid of a camera lucida.

Fig. 1. Mature compound cephalosporium in *Clonostachys Araucaria*. Nutrient broth.  $\times 750$ .

Fig. 2. Incipient phialide in *Gliocladium penicilloides*. Glycerine agar.  $\times 750$ .

Figs. 3-4. Basophilic granules in phialides of *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 5. Exudation of mucilage in *Clonostachys Araucaria*. Nutrient broth hanging drop.  $\times 1250$ .

Fig. 6. Phialide enclosed in mucilage in *C. Araucaria*. Endo's agar.  $\times 750$ .

Fig. 7. Orientation of granules at tips of phialides, and cleavage vacuoles in *Gliocladium penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 8. Splitting of phialide tip in *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Figs. 9-10. Emergence of conidia in *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 11. Endoconidia in *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 12. Twisted phialide with uninucleate endoconidia in *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 13. Mature uninucleate conidium of *G. penicilloides*. Glycerine agar.  $\times 1250$ .

Fig. 14. Conidiophores with endoconidia, and bi-vacuolate spores in *Clonostachys Araucaria* var. *confusa*. Litmus milk.  $\times 1250$ .

Fig. 15. Phialides of *Gliocladium penicilloides* from paraffin sections at  $3\ \mu$ . Glycerine agar.  $\times 1250$ .

Fig. 16. Constriction of spore mass during exit in *G. penicilloides*. Litmus milk.  $\times 1000$ .

Fig. 17. Diagram showing successive production of conidia, from observations at the end of 10, 20, 35, 65, and 70 minutes in *Clonostachys Araucaria*. Sabouraud's dextrose agar.

Figs. 18-28. *Allescheria Boydii*.

Fig. 18. Submerged chlamydospore. Nitrate agar.  $\times 750$ .

Fig. 19. Conidium. Raulin's agar.  $\times 750$ .

Figs. 20-21. Stages of development of submerged cephalosporia. Sabouraud's dextrose agar.  $\times 350$ .

Fig. 22. Coremium stage. Sabouraud's dextrose agar.  $\times 1250$ .

Fig. 23. Submerged lateral spore. Raulin's agar.  $\times 1250$ .

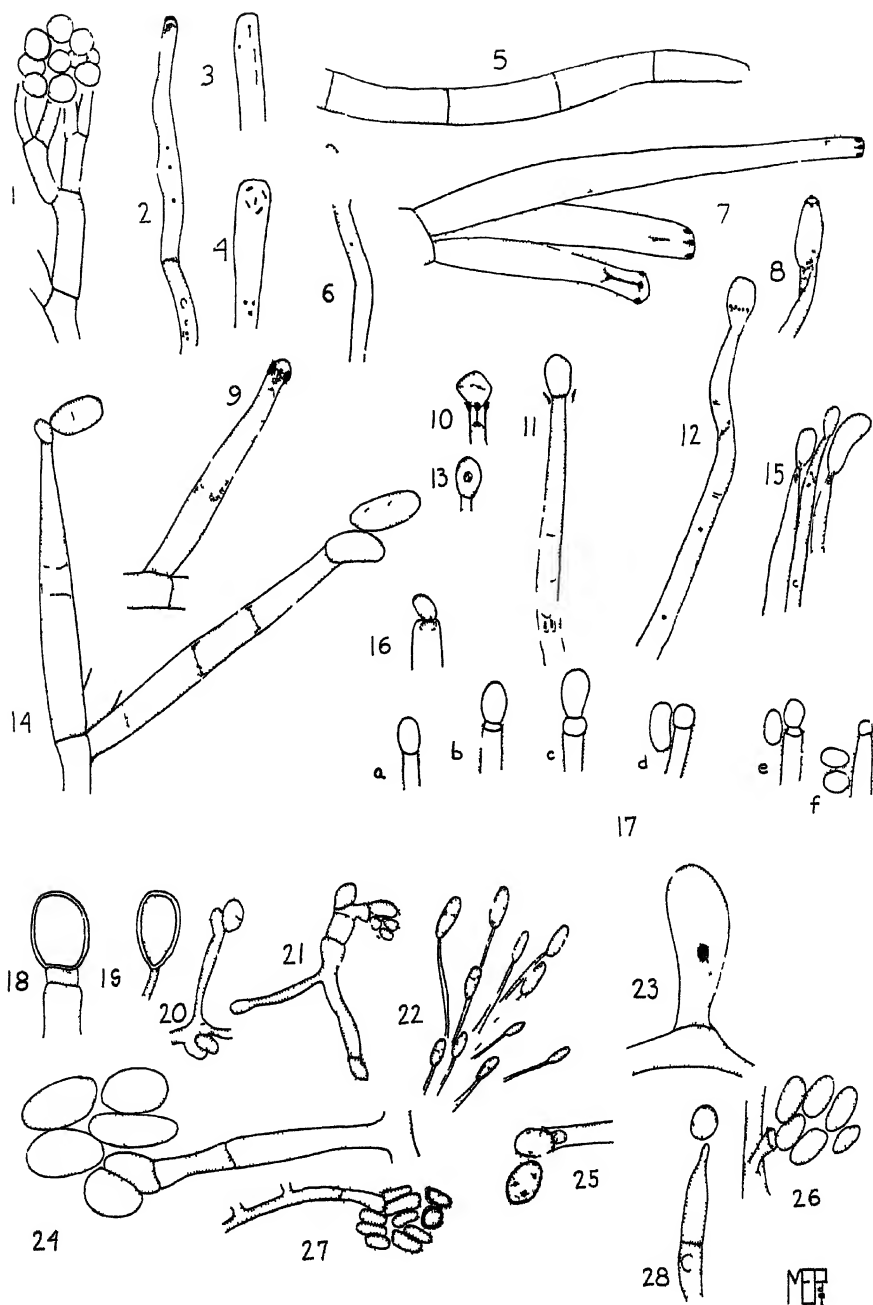
Fig. 24. Cephalosporium. Sabouraud's dextrose agar.  $\times 1250$ .

Fig. 25. Mature and young spore. Sabouraud's dextrose agar.  $\times 350$ .

Fig. 26. Lateral cephalosporium. Sabouraud's dextrose agar.  $\times 1250$ .

Fig. 27. Young and mature spores in cephalosporium. Raulin's agar.  $\times 350$ .

Fig. 28. Conidiophore. Raulin's agar.  $\times 1250$ .



## EXPLANATION OF PLATE

## PLATE 2

Unless otherwise stated, all drawings were made with the aid of a camera lucida.

Figs. 1-11. *Cephalosporium Serrae*.

- Fig. 1. Terminal chlamydospore. Potato agar.  $\times$  1250.
- Fig. 2. Series of chlamydospores. Potato agar.  $\times$  750.
- Fig. 3. Chlamydospores. Corn meal agar.  $\times$  750.
- Fig. 4. *Cephalosporium* within medium. Raulin's agar.  $\times$  1250.
- Fig. 5. Twisted phialide with endoconidia. Sabouraud's dextrose agar.  $\times$  1250.
- Fig. 6. Phialide with vacuoles. Sabouraud's dextrose agar.  $\times$  1250.
- Fig. 7. Dimorphic cephalosporium. Maltose agar. Not camera lucida.
- Fig. 8. Diagram of fructification.
- Fig. 9. Germinating chlamydospore. Nutrient broth.  $\times$  750.
- Fig. 10. Mucilage drop. Nutrient broth.  $\times$  750.
- Fig. 11. Packet type of cephalosporium. Nutrient broth.  $\times$  750.

Figs. 12-16. *Cephalosporium niveolanosum*.

- Fig. 12. Terminal chlamydospore.  $\times$  750.
- Fig. 13. Chlamydospores. Corn meal agar.  $\times$  750.
- Fig. 14. Phialide with endoconidia. Nutrient agar.  $\times$  750.
- Fig. 15. Phialide producing spore. Nutrient agar.  $\times$  750.
- Fig. 16. Young cephalosporium. Nutrient agar.  $\times$  750.

Figs. 17-21. *Cephalosporium Stuehmeri*.

- Fig. 17. Conidiophore with endoconidium. Sabouraud's dextrose agar.  $\times$  750.
- Fig. 18. Diagram of fructification.
- Fig. 19. Terminal chlamydospore. Corn meal agar.  $\times$  750.
- Fig. 20. Chlamydospores. Sabouraud's dextrose agar.  $\times$  350.
- Fig. 21. Peculiar aerial spore. Sabouraud's dextrose agar.  $\times$  350.

Figs. 22-25. *Cephalosporium rubrobrunneum*.

- Fig. 22. Origin of phialides from ropes of hyphae. Glycerine agar.  $\times$  350.
- Fig. 23. Slanted spore cluster. Sabouraud's dextrose agar.  $\times$  350.
- Fig. 24. Young cephalosporium. Sabouraud's dextrose agar.  $\times$  350.
- Fig. 25. Uninucleate spore. Sabouraud's dextrose agar.  $\times$  350.

Figs. 26-31. *Cephalosporium kiliense*.

- Fig. 26. Diagram of fructification. Endo's agar.
- Fig. 27. *Cephalosporium*.  $\times$  350.
- Fig. 28. Packet cephalosporium. Sabouraud's dextrose agar. Not camera lucida.

- Fig. 29. *Cephalosporium*. Sabouraud's dextrose agar.  $\times$  350.
- Fig. 30. Chlamydospores. Corn meal agar.  $\times$  1250.
- Fig. 31. Chlamydospores. Malt extract broth.  $\times$  1250.

Figs. 32-38. *Cephalosporium symbioticum*.

- Fig. 32. Chlamydospore. Glycerine agar.  $\times$  750.
- Fig. 33. Conidium. Nutrient broth.  $\times$  1250.
- Fig. 34. *Cephalosporia*. Endo's agar.  $\times$  600.
- Fig. 35. Conidia. Nutrient agar.  $\times$  1250.
- Fig. 36. Young submerged growth. Sabouraud's dextrose agar.  $\times$  1250.
- Fig. 37. Submerged growth on wort agar.  $\times$  1250.

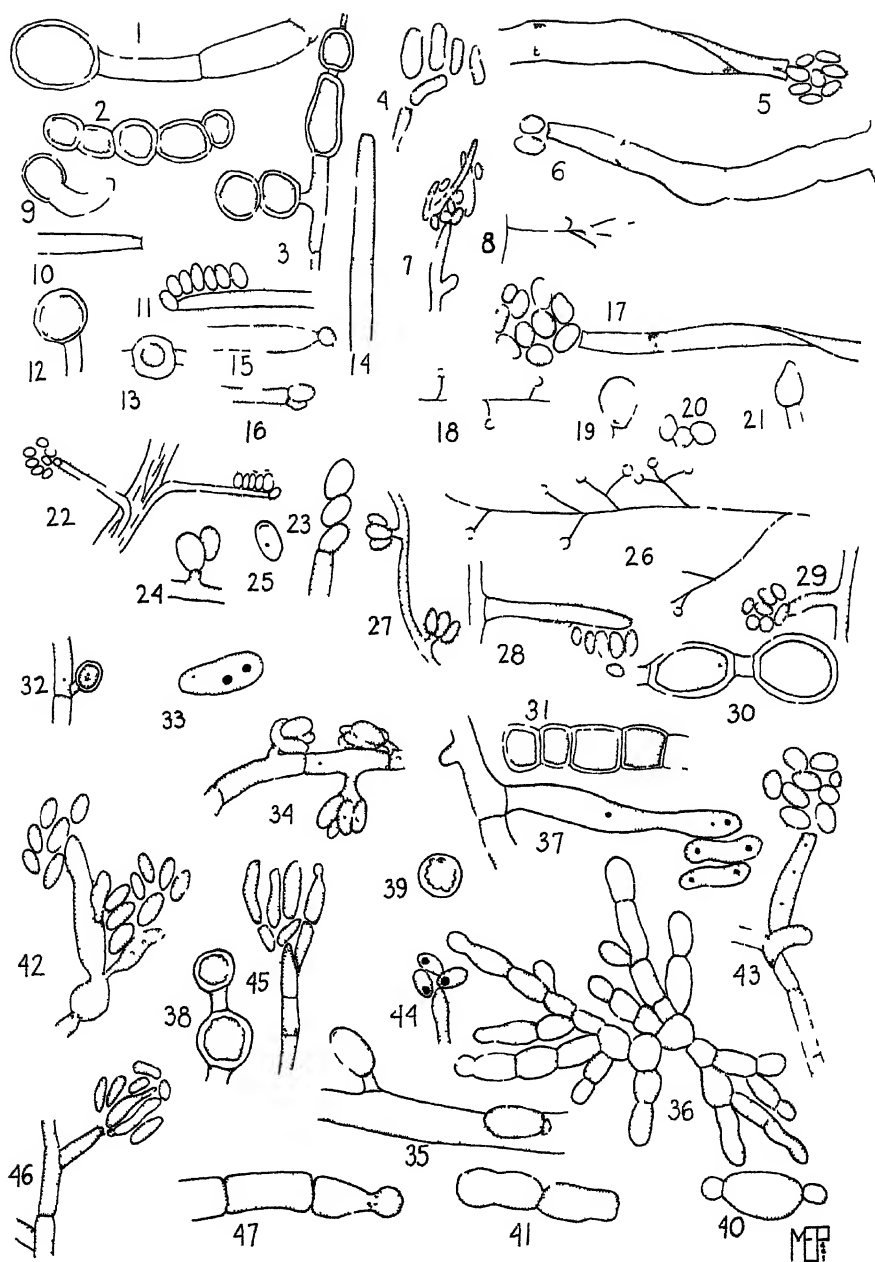




## EXPLANATION OF PLATE

PLATE 2 (*Continued*)

- Fig. 38. Chlamydospores. Sabouraud's dextrose agar.  $\times 1250$ .  
Figs. 39-44. *Torulopsis mucilaginos*a.  
Fig. 39. Resting cell. Malt extract broth.  $\times 750$ .  
Fig. 40. Bipolar budding. Malt extract broth.  $\times 750$ .  
Fig. 41. Submerged pseudomycelium. Nitrate agar.  $\times 750$ .  
Fig. 42. Pseudomycelium and irregular spore clusters. Endo's agar.  $\times 600$ .  
Fig. 43. Submerged cephalosporium. Nitrate agar.  $\times 750$ .  
Fig. 44. Submerged sporiferous tip. Nitrate agar.  $\times 750$ .  
Figs. 45-46. *Cephalosporium symbioticum*.  
Fig. 45. Cephalosporium with spore germinating *in situ*. Wort agar.  $\times 1250$ .  
Fig. 46. Cephalosporium. Wort agar.  $\times 1250$ .  
Fig. 47. Submerged mycelium of *Torulopsis mucilaginos*a, forming new cell by constriction.  $\times 1250$ .



## EXPLANATION OF PLATE

## PLATE 3

Drawings made with the aid of a camera lucida.

Figs. 1-19. *Gliocladium penicilloides*.

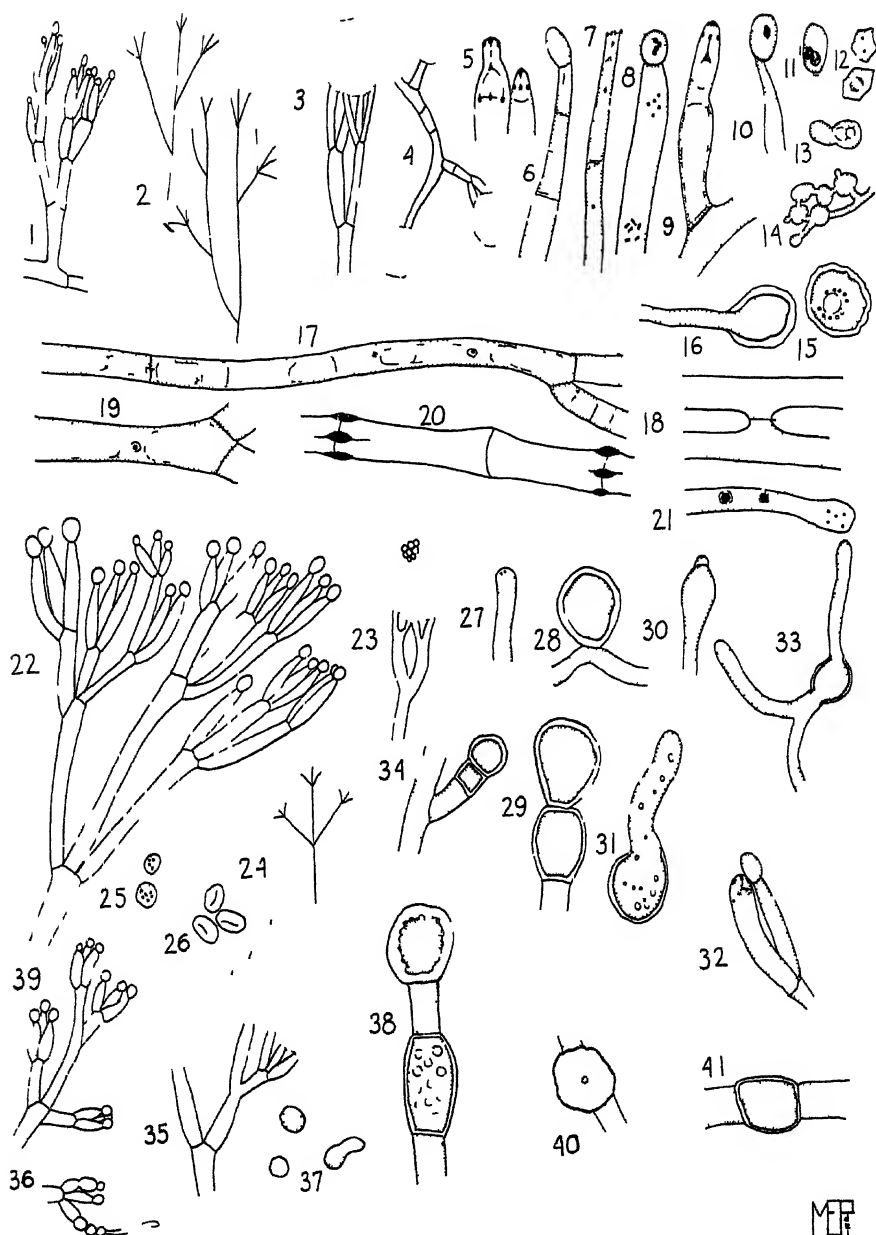
- Fig. 1. Conidiophore. Glycerine agar.  $\times 350$ .
- Fig. 2. Diagram of fructification.
- Fig. 3. Cephalosporium. Nutrient broth.  $\times 350$ .
- Fig. 4. Cephalosporia. Nutrient broth.  $\times 600$ .
- Fig. 5. Phialides with basophilic granules. Glycerine agar.  $\times 1250$ .
- Fig. 6. Phialide with mature spore and endoconidia. Glycerine agar.  $\times 1250$ .
- Fig. 7. Phialide with broken tip. Glycerine agar.  $\times 1250$ .
- Fig. 8. Phialide with basophilic granules. Glycerine agar.  $\times 1250$ .
- Fig. 9. Phialide with basal vacuole. Glycerine agar.  $\times 1250$ .
- Fig. 10. Conidium. Glycerine agar.  $\times 1250$ .
- Fig. 11. Conidia showing granular material. Glycerine agar.  $\times 1250$ .
- Fig. 12. Conidia. Glycerine agar.  $\times 1250$ .
- Fig. 13. Germinating conidium. Glycerine agar.  $\times 750$ .
- Fig. 14. Fusions of germ tubes of conidia. Nutrient broth.  $\times 350$ .
- Fig. 15. Akinete. Glycerine agar.  $\times 750$ .
- Fig. 16. Germinating akinete. Glycerine agar.  $\times 750$ .
- Fig. 17. Hypha. Glycerine agar.  $\times 1250$ .
- Fig. 18. Hyphal fusions. Nutrient broth.  $\times 1250$ .
- Fig. 19. Sub-phialide cell. Glycerine agar.  $\times 1250$ .

Figs. 20-32. *Gliocladium deliquescens*.

- Fig. 20. Submerged mycelial cell showing granular bodies at septa. Glycerine agar.  $\times 1250$ .
- Fig. 21. Tip of mycelial cell with large dancing bodies and small terminal granules. Nutrient broth.  $\times 1250$ .
- Fig. 22. Young conidiophore. Glycerine agar.  $\times 1000$ .
- Fig. 23. Cephalosporium.  $\times 350$ .
- Fig. 24. Diagram of cephalosporium branching structure.
- Fig. 25. Conidia with chromatic material. Glycerine agar.  $\times 1250$ .
- Fig. 26. Conidia from smear stained with gentian violet.  $\times 1250$ .
- Fig. 27. Aerial hypha with granular tip. Glycerine agar.  $\times 1250$ .
- Fig. 28. Chlamydospore (?). Sabouraud's dextrose agar.  $\times 800$ .
- Fig. 29. Chlamydospores. Glycerine agar.  $\times 1000$ .
- Fig. 30. Aborted ascogonium (?). Glycerine agar pH 3.8.  $\times 350$ .
- Fig. 31. Germinating akinete. Sabouraud's dextrose agar.  $\times 750$ .
- Fig. 32. Phialide with terminal granules. Glycerine agar.  $\times 1250$ .

Figs. 33-41. *Gliocladium fimbriatum*.

- Fig. 33. Germinating conidium. Endo's agar.  $\times 600$ .
- Fig. 34. Chlamydospores. Sabouraud's dextrose agar.  $\times 600$ .
- Fig. 35. Conidiophore. Corn meal agar.  $\times 750$ .
- Fig. 36. Dimorphic fructification. Sabouraud's dextrose agar.  $\times 350$ .
- Fig. 37. Conidia. Sabouraud's dextrose agar.  $\times 750$ .
- Fig. 38. Akinetes. Glycerine agar.  $\times 750$ .
- Fig. 39. Conidiophore. Sabouraud's dextrose agar.  $\times 350$ .
- Fig. 40. Akinete upon addition of alcohol and chloroform, showing dissolution of oil.  $\times 750$ .
- Fig. 41. Intercalary chlamydospores. Corn meal agar.  $\times 750$ .



## EXPLANATION OF PLATE

## PLATE 4

Drawings made with the aid of a camera lucida.

Figs. 1-14. *Glocladium Vermoeseni*.

Fig. 1. Submerged chlamydospores. Sabouraud's dextrose agar.  $\times 350$ .

Fig. 2. Aerial chlamydospores. Raulin's agar.  $\times 750$ .

Fig. 3. Endoconidial method of formation of chlamydospores. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 4. Arthrospores. Corn meal agar.  $\times 750$ .

Fig. 5. Conidiophore. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 6. Mature conidium. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 7. Part of cephalosporium showing exterior thick granular layer of mucus and spores deformed by pressure. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 8. Branch of penicillate fructification. Czapek's agar.  $\times 350$ .

Fig. 9. Conidiophores. Corn meal agar.  $\times 750$ .

Fig. 10. Unusual conidiophore. Raulin's agar.  $\times 750$ .

Fig. 11. Oidia (?). Raulin's agar.  $\times 750$ .

Fig. 12. Anomalous structure. Raulin's agar.  $\times 1250$ .

Fig. 13. Diagram of fructification.

Fig. 14. Submerged akinete. Raulin's agar.  $\times 750$ .

Figs. 15-26. *Clonostachys Araucaria* var. *confusa*.

Fig. 15. Conidiophore. Czapek's agar.  $\times 350$ .

Fig. 16. Conidiophore with warts. Czapek's agar.  $\times 350$ .

Fig. 17. Short lateral cephalosporium. Sabouraud's dextrose agar.  $\times 350$ .

Fig. 18. Phialides with endoconidia. Endo's agar.  $\times 1000$ .

Fig. 19. Chlamydospore (?). Sabouraud's dextrose agar.  $\times 600$ .

Fig. 20. Dimorphic fructification. Lactose broth.  $\times 600$ .

Figs. 21-22. Copulating conidia. Litmus milk.  $\times 1250$ .

Fig. 23. Mature conidium.  $\times 750$ .

Fig. 24. Germinating conidium. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 25. Hyphal fusions. Endo's agar.  $\times 350$ .

Fig. 26. Submerged chlamydospore. Raulin's agar.  $\times 750$ .

Figs. 27-31. *Clonostachys Araucaria* var. *rosea*.

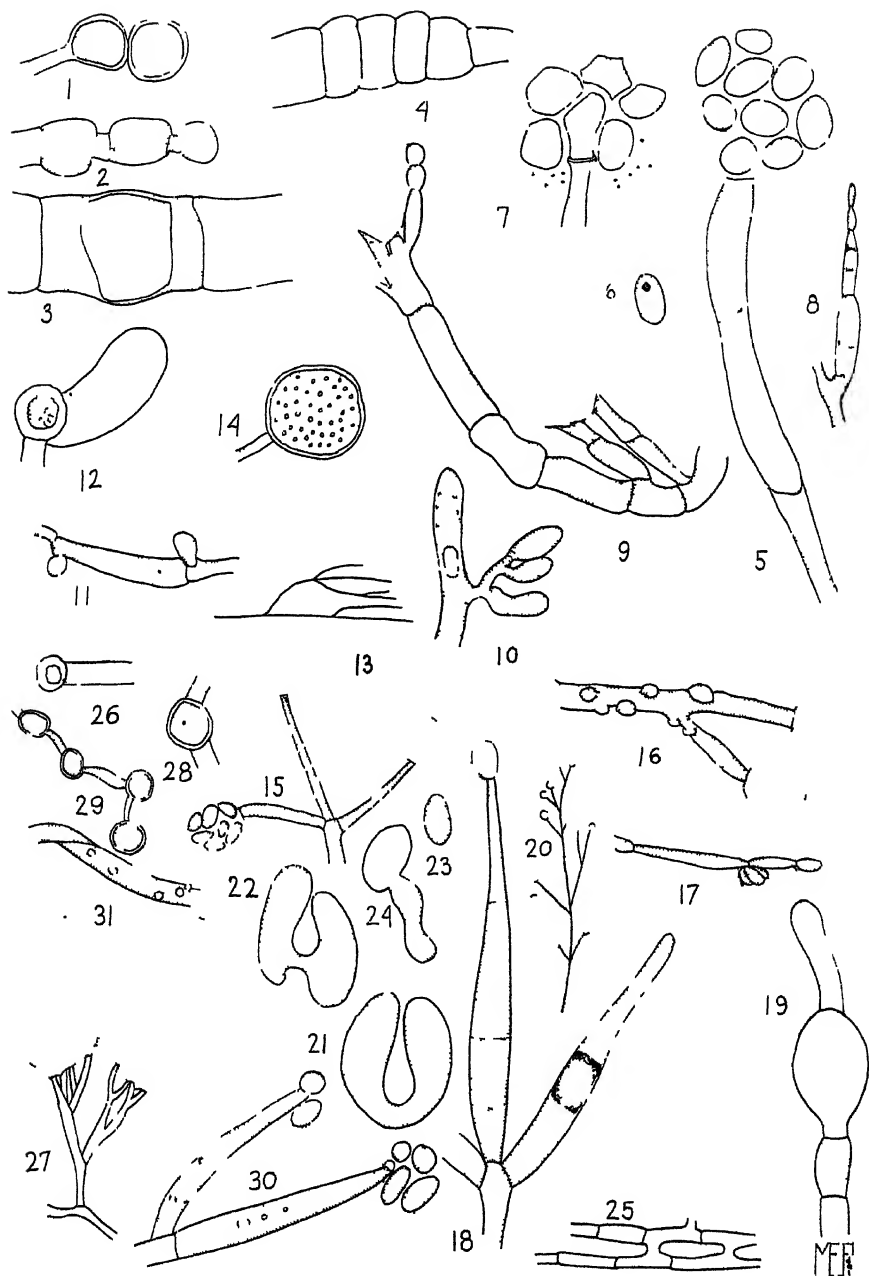
Fig. 27. Cephalosporia. Endo's agar.  $\times 250$ .

Fig. 28. Chlamydospore. Corn meal agar.  $\times 750$ .

Fig. 29. Submerged chlamydospores (?). Wort agar.  $\times 350$ .

Fig. 30. Phialides with endoconidia. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 31. Hypha with warts. Sabouraud's dextrose agar.  $\times 750$ .



## EXPLANATION OF PLATE

## PLATE 5

Drawings made with the aid of a camera lucida.

Figs. 1-7. *Clonostachys spectabilis*.

Fig. 1. Terminal chlamydospores. Cherry agar.  $\times 750$ .

Fig. 2. Intercalary chlamydospore. Malt extract broth.  $\times 750$ .

Fig. 3. Submerged terminal cell (?). Malt extract broth.  $\times 750$ .

Fig. 4. Botrytis type of spore. Sabouraud's dextrose agar.  $\times 350$ .

Fig. 5. Same. Corn meal agar.  $\times 350$ .

Fig. 6. Mycelium associated with Botrytis type of fructification. Czapek's agar.  $\times 350$ .

Fig. 7. Spores. Corn meal agar.  $\times 750$ .

Figs. 8-13. *Scopulariopsis brevicaulis*.

Fig. 8. Young conidium before putting down endogenous wall. Nutrient agar.  $\times 1250$ .

Fig. 9. Mature conidium and phialide showing segmentation. Nutrient agar.  $\times 1250$ .

Fig. 10. Conidium. Nutrient agar.  $\times 1250$ .

Fig. 11. Branched conidiophore. Nutrient broth.  $\times 1250$ .

Fig. 12. Phialide with conidia. Nutrient agar.  $\times 1250$ .

Fig. 13. Conidia. Nutrient agar.  $\times 1250$ .

Figs. 14-26. *Clonostachys Draucaria*.

Fig. 14. Chlamydospores. Corn meal agar.  $\times 750$ .

Fig. 15. Mycelium with warts. Sabouraud's dextrose agar.  $\times 750$ .

Fig. 16. Dimorphic conidiophore.  $\times 350$ .

Fig. 17. Cephalosporium and phialide with endoconidia.  $\times 1250$ .

Fig. 18. Phialide with twisted walls. Sabouraud's dextrose agar.  $\times 600$ .

Fig. 19. Fructification like Corda's type. Sabouraud's dextrose agar.  $\times 1250$ .

Fig. 20. Diagram showing a type of branching.

Fig. 21. Another type of branching.

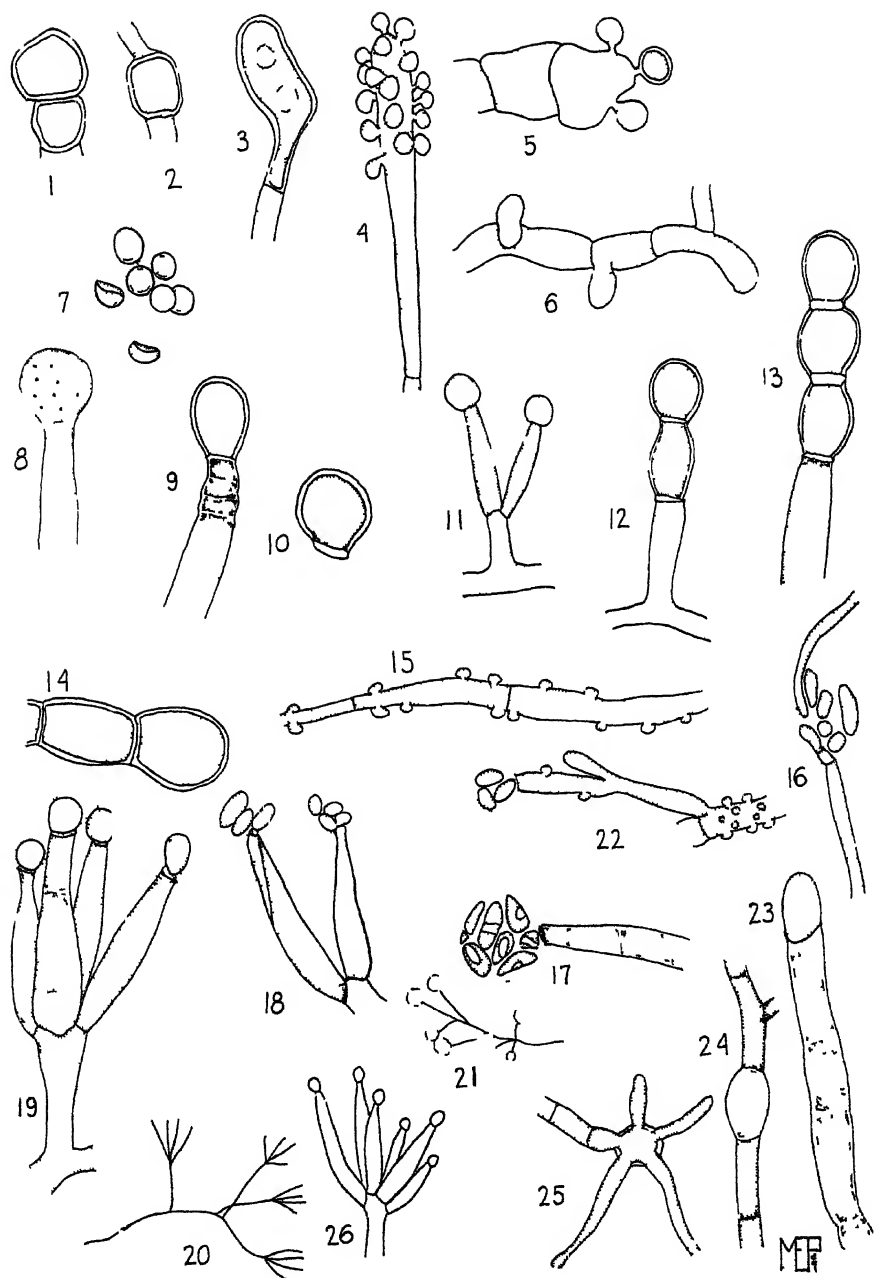
Fig. 22. Phialide with warts. Czapek's agar.  $\times 350$ .

Fig. 23. Endoconidia. Sabouraud's dextrose agar.  $\times 1250$ .

Fig. 24. Intercalary chlamydospore. Lactose broth.  $\times 600$ .

Fig. 25. Germinating conidium. Lactose broth.  $\times 600$ .

Fig. 26. Conidiophore with six concurrent branches. Wort agar.  $\times 600$ .





## EXPLANATION OF PLATE

## PLATE 6

Figs. 1-14, giant colonies on Czapek's agar.

Fig. 1. *Cephalosporium niveolanosum*

Fig. 2. *Cephalosporium symbioticum*

Fig. 3. *Gliocladium deliquescens*

Fig. 4. *Gliocladium fimbriatum*

Fig. 5. *Gliocladium penicilloides*

Fig. 6. *Gliocladium Vermoeseni*

Fig. 7. *Allescheria Boydii*

Fig. 8. *Clonostachys Araucaria* var. *confusa*

Fig. 9. *Cephalosporium rubrobrunneum*

Fig. 10. *Clonostachys Araucaria* var. *rosea*

Fig. 11. *Clonostachys Araucaria*

Fig. 12. *Cephalosporium küiense*

Fig. 13. *Cephalosporium Serrae*

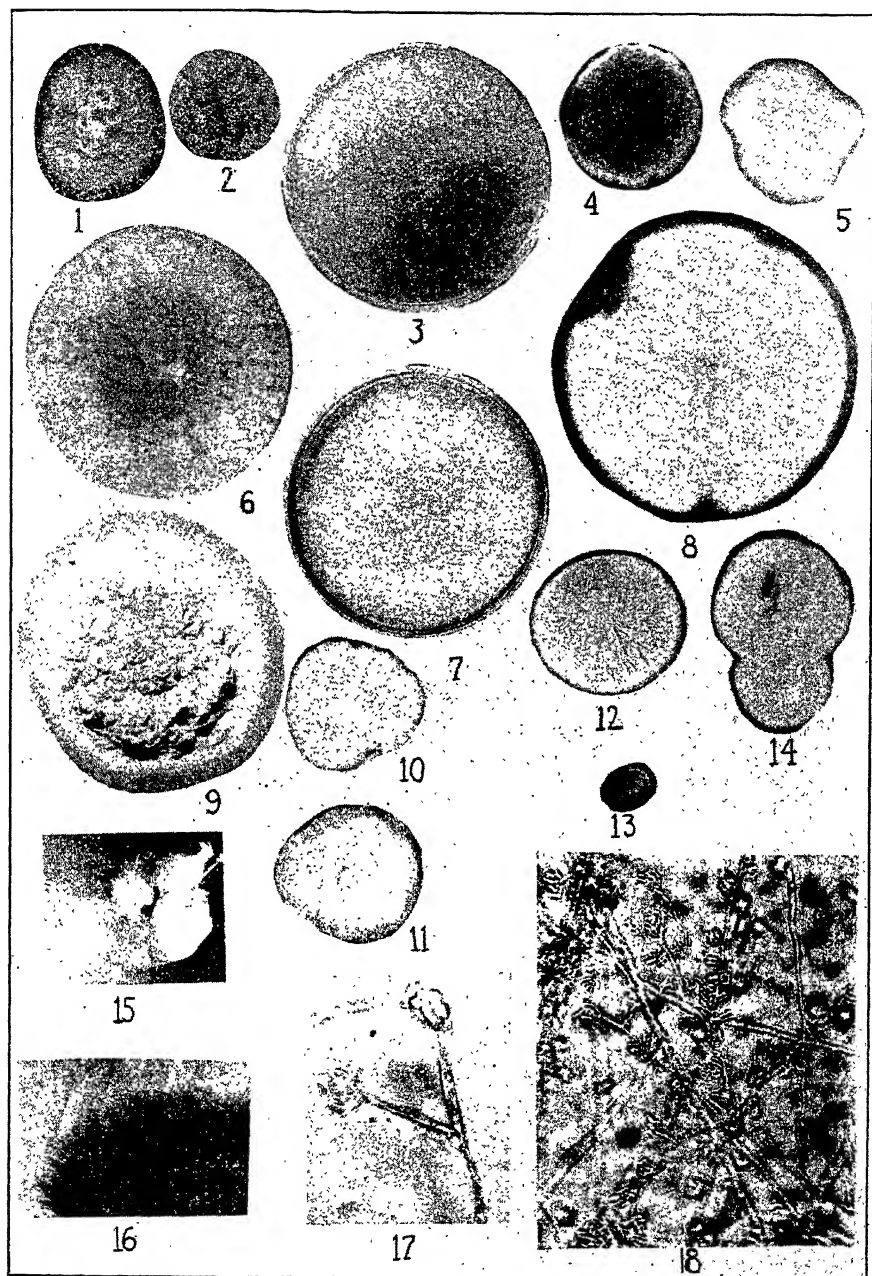
Fig. 14. *Cephalosporium Stuehmeri*

Figs. 15-18, photomicrographs.

Figs. 15-16. Granular incrustations of *Cephalosporium rubrobrunneum* upon blood serum.

Fig. 17. Branched conidiophore of *Clonostachys Araucaria* with warts and cephalosporia.  $\times 1000$ .

Fig. 18. Agar micro-culture showing cephalosporia in *Cephalosporium symbioticum*.  $\times 1000$ .



PINKERTON — CONIDIAL FORMATION



# A STUDY OF THE GENUS *HELICOGLOEA*<sup>1</sup>

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A paper published by Patouillard in 1892 included amongst the heterobasidiomycetes the new genus *Helicogloea*, represented by a single species—*H. Lagerheimi* Pat. Later Patouillard seemed confused and uncertain as to its true identity and eventually, in a letter to Coker ('20), stated that *Helicogloea* was not distinct from *Platyglea*. In the literature subsequent references are based on Patouillard's work. No one seems to have examined the type. Just as this work was going to press under the name of *Saccoblastia*, Dr. Donald Rogers called attention to the type which is now in the Farlow herbarium. Patouillard's description fails to mention the "sac" or hypobasidium, easily the most conspicuous part of the fructification. From his illustrations one is forced to conclude that although Patouillard was aware of the structure he was unable to interpret it. There can be no doubt as to the real nature of the specimen. Not only is it a good genus but the type of what three years later Möller ('95) called *Saccoblastia*. Since Patouillard's formal description does not include a statement concerning the hypobasidia the genus stands in need of emendation. Accordingly, the recognized species of *Saccoblastia* must be transferred to the older genus, *Helicogloea*.

*HELICOGLOEA* Pat., emend.

Fructification resupinate, indeterminate, ranging from a very thin film to a layer several mm. thick, mucous-gelatinous or

<sup>1</sup> An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

floccose; hyphae with or without clamp connections, 2–6  $\mu$  wide, branched, sometimes anastomosing, attenuated at the septa; basidia heteromorphic, terminal or intercalary in origin; hypobasidia conspicuous, saccate lateral (with one exception) expansions of the basidial primordia sometimes variously constricted, 15–20–58  $\times$  4.5–8–16  $\mu$ ; epibasidia cylindrical outgrowths of the primordia or hypobasidia, expanding apically to the sporogenous portion, articulate-geniculate, 3–4-septate, each segment producing a sterigma and spore, or an accessory appendage eventually tipped by a sterigma and spore, the entire basidium 45–140  $\times$  4–11  $\mu$ ; spores hyaline, ovoid to ellipsoid, often flattened on one side, with a prominent blunt lateral apiculus, 7–19  $\times$  4–13  $\mu$ ; germination by repetition.

*Helicogloea* is a member of the Auriculariaceae, heterobasidiomycetes which bear basidiospores in linear sequence on transversely septate basidia. The genus, by reason of a curious sac-like appendage produced during basidial ontogeny, has always been noteworthy. Since the first clear morphological account (Möller, '95) several species have been described but little detailed information concerning the developmental cycle has accumulated. Gäumann and Dodge ('28) summarize the situation by saying: "A cytological study of the species is needed for the interpretation of this storage organ which is unknown in other groups of fungi."

In 1895 Möller (*l. c.*) described two species collected during a stay in Brazil. Both possessed the unique saccate hypobasidia. Möller completely delineated the morphology of the genus. Further detailed studies were not made. As apparently Patouillard's material was never questioned, this work of Möller's stood as the standard of the genus *Saccoblastia*, represented by the species *S. ovispora* Möll. and *S. sphaerospora* Möll.

The next record is that of Bresadola ('03), who added a species from Poland, *Helicogloea graminicola*. His description was accompanied by neither detailed studies nor illustrations. Likewise Bourdot and Galzin ('09, '28), who have enlarged the genus by several species and varieties, have contributed only taxonomic observations.

The first collection of the genus in the United States was made by Couch, 1920, in North Carolina. Coker ('20), puzzled by its peculiar characters, which were so suggestive of *Helicogloea Lagerheimi* yet differing in several respects, published a description of the fungus as *Saccoblastia ovispora* Möller var. *caroliniana*. In 1928, in the meantime having consulted Bresadola who supposedly had seen the type of the species in question, he decided to recognize it as an autonomous species, now *Helicogloea caroliniana*. The original description includes a careful morphological account with lucid illustrations.

Linder ('29) announced a new species based on material collected in Cuba, *Helicogloea intermedia*. This remarkable form was found to have two types of basidial development, the so-called "clavate" type in addition to the established saccate one. From his preparations Linder was able to augment considerably the cytological data. But even so they remained far from complete. The condition of his material which had been preserved in 70 per cent alcohol was hardly suitable for critical work.

*Helicogloea Lagerheimi* Pat. was collected in Iowa during the summer of 1932 by Rogers and later reported by him ('33). He made additional gatherings during the summer of 1934 and at both times killed and fixed samples of a number of collections. It is material from these sources upon which this study is based.

#### TECHNIQUE

Several collections of fresh material of *Helicogloea Lagerheimi* were available for histological preparations. All of them were killed and fixed in Flemming's weaker fluid. To the fixing fluid for two lots was added 1 per cent maltose. For two others dehydration by a butyl series was employed, whereas the first mentioned were run through Chamberlain's ('32) full alcohol schedule to xylol and paraffin. Those of the maltose-xylol series proved the most valuable for critical stages. However, subsequent examination indicated that variation was due to the particular specimen as much as to fixation. Serial sections were cut at 15, 10, 8, and 5  $\mu$ . Various stains were tried but

Haidenhain's iron-alum haematoxylin with a counter stain of phloxine (a 1 per cent solution in 95 per cent alcohol) was used almost exclusively. A few slides were prepared with Fleming's triple stain to serve as a check for the presence of septa at certain points. In addition whole mounts were made of herbarium specimens whenever possible. After these were revived in a moist chamber they were treated with a weak solution of potassium hydroxide and stained with phloxine (1 per cent solution in water).

#### MORPHOLOGY OF *H. LAGERHEIMI*

The indeterminate fructification of *Helicogloea Lagerheimi* in a living condition, or when it has been revived in a moist-chamber, appears as a thin gelatinous or mucous coat, loosely attached to its substratum of decorticated and well-decayed wood of various sorts. It ranges in thickness from 100  $\mu$  to 1 mm. From prepared sections it is evident that the penetration within the substratum is slight. A few scattered hyphal threads are all that appear within the wood cells, and these are never deeper than a few  $\mu$ .

Morphologically, there is no tissue differentiation into trama and hymenium, but the whole is simply a mass of hyphal and basidial elements loosely interwoven (fig. 19). This composite figure of the fructification as seen in section represents one in which the hyphae are practically parallel, a feature characteristic of lesser developed fructifications. The development of the fruiting body ranges from a thinly spread layer to thicker ones in which the basidial elements are restricted to the upper layer. In moderately developed specimens the fruiting layer may be as much as one-third the total, or in better developed ones as little as one-sixth, as shown by the comparative scales (fig. 20). The fruiting region is the actively growing part, bearing basidia singly at various levels. The individual hyphal cells are typically binucleate. Occasionally some cells are four-nucleate, but this merely indicates a recent nuclear division not yet followed by wall formation (fig. 14a, d). Usually the two processes are concurrent. The nuclei may lie

in close approximation or be widely separated within the same cell. As the cells become more mature the protoplasmic content is reduced, sometimes to only scattered remnants about the nuclei (fig. 14b, c). The mycelium is slightly irregular, characteristically attenuated at the septa, and its individual cells vary considerably in length. Branches arise as lateral outgrowths of a cell and receive daughter nuclei of the parent-cell dikaryon (fig. 15). There are no clamp connections, but the hyphae branch freely. Anastomoses also occur, although there is no evidence to support Linder's contention that such hyphal union carries a sexual stimulus to fructification.

The morphological development of the basidium may be followed in the diagrammatic series, figures 1 to 13 inclusive, and seen in summation in the composite illustration, figure 19. These figures, drawn to a common scale, show the entire cycle. The first indication of basidium production is the cutting off of a terminal hyphal cell, the primordial cell, easily distinguished by its more homogeneous and denser staining protoplasm (figs. 15, 1). It contains two nuclei, descendants of the dikaryon of the subterminal cell. There may be additional basidia produced by proliferation of the subterminal cell (fig. 16), just as shown by Möller in *H. Lagerheimi* and Coker in *H. caroliniana*. After an increase in thickness the primordium pushes out a small lateral protuberance just above the basal septum (fig. 2). This enlarges rapidly to become the "sac," or, as it will be designated henceforth, the hypobasidium, *sensu* Neuhoff ('24) (figs. 3, 4, 5, 6). Into this the two nuclei migrate and subsequently fuse.

Following a rather protracted resting period the fusion nucleus migrates from the hypobasidium, passing back through the primordial cell into the epibasidium, again *sensu* Neuhoff (fig. 7). The latter, an outgrowth of the primordium, may be apparent at an early stage. Furthermore, it may be distinctly elongated at the time the nuclei leave the hypobasidium or it may develop more slowly (figs. 7, 25). Between the primordium and the epibasidium there is commonly a conspicuous crimp or constriction, but never a wall (fig. 17). The epibasid-



ium is usually elongating as the nucleus moves along (fig. 8), and when it has attained its mature length the apical portion thickens and bends over (figs. 9, 10). Accompanying this is a complete evacuation and withering of the hypobasidium. Later the withering includes the primordial part, and eventually it extends to the lower portion of the epibasidium itself (figs. 11, 12). In mounts made with KOH these emptied portions may be quite swollen so that no collapse is apparent, but the regions are entirely drained of protoplasm. The nucleus now divides, the first septum coming in at once. In a short time the two daughter nuclei divide, and the typical segmented basidium is formed with four sterigmata and spores. These are so oriented commonly, through the curvature of the epibasidium, that the sporogenous portion lies procumbent on the surface of the fructification, thereby greatly favoring the chances of spore dispersal (figs. 12, 13). Bends are located below the spore-bearing portion or in it and simply adjust this region for favorable discharge (figs. 23, 63b). Excessively long thickened appendages in place of sterigmata occur frequently, but these eventually give rise to true sterigmata and spores (fig. 67b, c, d). Infrequently the basidia remain erect, in which case appendages take care of the spore orientation or if the sporogenous portion is unobstructed at the surface it need produce only sterigmata.

As would be expected, there is considerable variation in the morphology of the basidium and its parts. The lateral hypobasidium or "sac," the most conspicuous feature of the fructification, is typically oblong-ovoid, but often it is constricted once or more (fig. 18a, b), a condition culminating perhaps in the extremes illustrated by *f* and *g* of the same figure. It should be noted that the general orientation of the fructification is such that the hypobasidia are only rarely pendent as extant accounts say. The fructification is resupinate, commonly effused on the under side of logs, hence the general configuration is to be construed inversely to the usual interpretation (fig. 19). Usually the epibasidium originates from a terminal primordial cell as a vertical outgrowth from it, but occasionally it seems to have

been produced directly from the proximal end of the hypobasidium. The latter situation would then be equivalent to what apparently is the rule rather than the exception in *H. intermedia*. After examining Linder's material and his illustrations it is quite clear that there is a real difference in the origin of the basidial components of these two species. In *H. Lagerheimi* those hypobasidia which seemingly are not borne on terminal primordia with subsequent elongation of the epibasidia, but which appear to produce their epibasidia directly at their proximal end, are in reality borne on primordia which are short lateral branches of a proliferating complex. Hence their true origin is from a single terminal cell from which the hypobasidium arises in the ordinary fashion. This is clearly substantiated by the position of the walls (cf. figs. 21a, b; 75a, b). In *H. intermedia* one can easily trace the origin of the saccate type of hypobasidium from an intercalary binucleate cell which pushes out the hypobasidium, just as in *H. Lagerheimi*, and it in turn produces proximally the epibasidium (fig. 75b, c, d). There is, then, a fundamental difference between these two species in regard to the position and origin of the basidium and its components. In either species the type of development characteristic for one may occur as a rare exception in the other. Whether the primordium be terminal or intercalary, it is always distinguishable by its denser protoplasmic content. A study of *H. caroliniana*, *H. Lagerheimi*, and *H. graminicola* reveals that they are essentially identical at these stages. A third variation occurs in *H. pinicola*. Here the primordium is intercalary, but the epibasidium originates with a lateral outpushing of the primordium, usually more or less apical, rather than from the proximal germination of the hypobasidium (fig. 72b, c). No case of distal germination of the hypobasidium, such as Linder reported in his work, has been noticed in any of the material examined.

Quite early the budding epibasidium is visible at the apical end of the primordium. It is seldom distinguishable before the latter attains its mature diameter or previous to the formation of the hypobasidium, and it may not appear until much

later (cf. figs. 5, 22, 31b). Exceptionally, it is lateral in position. Its further development is either upright or variously bent, consequent upon its origin or the requirements for spore discharge (fig. 23). If there is a constriction between primordium and epibasidium it persists and is apparent in all stages, though there are numerous instances in which the epibasidium is little, if at all, distinct from the primordial portion (fig. 25b). The elongation of the epibasidium is various in relation to the accompanying nuclear behavior. It may follow one of three general patterns: I, The nucleus migrates from the hypobasidium as the epibasidium elongates (fig. 24); II, The elongation of the epibasidium distinctly precedes the nuclear migration (fig. 25a, b) which may be delayed until a stage as late as that shown in figure 10; III, Migration precedes elongation. In such event there is little if any protoplasmic evacuation of the hypobasidium until the epibasidium begins elongating (fig. 26a). The last scheme is infrequent except in less well developed fructifications. This results in a distinctly shorter basidium whose developmental sequence may be followed in figure 26b, c, d, and e. The other two types occur about equally, though type I probably represents the typical behavior. Type II seems more often associated with an extremely long unconstricted form of epibasidium and is undoubtedly a direct response to its location within the fructification. Types I and II intergrade. The type of behavior is consequent upon the primordium location. In general, if the primordium is near the surface there is no need for great elongation, but if it is well within the fructification the longer form necessarily results.

The crimp at the base of the epibasidium, though persistent, is never cut off by a wall. However, a second constriction is located characteristically just below the inflated sporogenous part. Such a joint has been noted by Coker in *H. caroliniana*; Wakefield and Pearson ('23) and Rogers ('34) show it in different degrees for *H. Lagerheimi*. According to Wakefield and Pearson there is no wall at this point; according to Rogers there is. Rogers' figures present a condition comparable to the one Coker noticed. In *H. Lagerheimi* three septa are found

more frequently than four in the sporogenous portion. Commonly, protoplasmic remnants simulate a basal wall, but the actual presence of a wall is exceptional (fig. 58). Ordinarily, the second constriction lies just behind the evacuation level of the fourth segment (figs. 12, 13, etc.); it may be accompanied by a bend. At times the constriction is very deep, and if in addition the fourth segment has a basal septum, the condition is identical with Rogers' illustration (fig. 27a, b). Whether the last segment does or does not have a basal wall, there is never any protoplasm left behind the segmented portion. In *H. caroliniana* the fourth septum is evident early in the development of the sporogenous portion (fig. 76b). Again the articulation receives varying emphasis so that one finds examples ranging from a definite joint, as Coker showed, to a simple bend.

#### CYTOLOGICAL OBSERVATIONS

Each hyphal cell characteristically contains two small nuclei whose position within the cell is various. The origin of the two-nucleate condition was not determined. As the cells grow older and elongate their protoplasmic content is much reduced until it may consist only of scant bits around the nuclei. The nuclei of the hyphae, however, remain small. Each nucleus is composed of a deeply staining central nucleolus embedded in the homogeneous nucleoplasm and is surrounded by a delicate membrane which is barely differentiated from the cytoplasm in which the whole lies. The apical cells destined to become the basidial primordia are limited to the more actively growing regions near the surface of the fructification. Their contents more nearly fill the cell and stain as an even, homogeneous mass. Consequently these primordia and the sub-adjacent cells are the most favorable places to locate mitosis. This is typically conjugate, both nuclei being entirely synchronized in behavior, though the smallness of the cells and of the nuclei at this stage makes detailed analysis practically impossible. At times one finds the spindles in the well-known side-by-side orientation or slightly oblique (fig. 28a). Curiously enough, in by far the

majority of cases the figures are crossed at varying angles (fig. 28b, c). Future orientation of the spindles in this way is implied clearly in the early stages shown by *a*, *b*, and *c* of figure 29. Such behavior is probably due to the small diameter of the cell which would prohibit a side-by-side arrangement. No additional details could be discerned except that the membrane has disappeared by the time of spindle formation, and sometimes the remnants of the nucleoli are visible in the nuclear cavity. Later they disappear (fig. 30). Following mitosis a wall is laid down between the two daughter dikaryons. This process may continue for several divisions but eventually the terminal cell constitutes the future primordium. The wall may not be formed immediately. In figure 31a, where it has just been laid down, the nuclei give evidence of a longer reorganization. Here, too, the cell contents are quite vacuolate, the result probably of rapid elongation and growth. The nuclei of the primordium are in a typical resting condition.

When first delimited the primordium is little distinguished in size from the hyphal cells. Before the production of the hypobasidium it increases in diameter and somewhat in length, though again it is difficult to evaluate this exactly in a form so variable in size and behavior. Examples in figure 32 represent an increase with reasonable surety, for they were approximately adjacent in the same section.

Beginning as a lateral outgrowth of the primordial cell just anterior to the basal septum, the hypobasidium rapidly assumes the form of an inflated sac-like appendage (figs. 31b, 33). At no time in its development is it without cytoplasm. As the hypobasidium elongates the nuclei in the primordium, which up to now have been more or less centrally located, enlarge slightly and prepare to move into the hypobasidium. They are now somewhat ellipsoidal. Sometimes the nuclei lie in such close association that they seem to be fusing, but careful focusing reveals that their individual membranes are intact (fig. 34a, b). One nucleus of the pair may precede the other into the hypobasidium by a considerable distance (fig. 35). In any event, the movement is always tandem, with the long axes

of the nuclei parallel to that of the primordium. There is no change in their shape as the nuclei pass through the narrow neck connecting hypobasidium and primordium. Following this migration the primordium is commonly more vacuolate (fig. 34b). Darker staining masses in the protoplasm are suggestive of a protoplasmic flow accompanying the nuclear passage (figs. 35, 37). Occasionally one nucleus of the pair may be larger, but this only signifies an earlier increase in its volume (fig. 38d, e). Once in the hypobasidium, the nuclei come together for fusion. Up to this time the hypobasidium has been growing but after karyogamy growth ceases. The two nuclei ordinarily do not penetrate below the mid-region of the hypobasidium, except in the case of the constricted hypobasidia where they always lie in the larger portion (fig. 18a, b, f, g). At the point of contact their membranes break down, allowing the components of the two nuclei to intermingle completely (fig. 38c). Usually until then their structure is no more differentiated than in the resting stage, although in figure 38d one nucleus is already forming a reticulum. A little later the fusion nucleus is dumb-bell-shaped but this constriction is transitory (fig. 39). The fusion nucleus is bounded by a continuous membrane; it contains two nucleoli, usually opposite each other, and a reticulum in varying degrees of advancement. The few variations of these earlier stages involve only minor deviations from the pattern. First, there is variability in the position of the nuclei in the hypobasidium. Figure 38e illustrates deeper penetration than usual. Another difference is that at times one nucleus is somewhat more advanced, as evidenced by its greater volume and earlier appearance of a reticulum (fig. 38e). In general these variations are rare, the migration and fusion processes being quite regular.

Within the fusion nucleus, now spherical in outline, the nucleoli draw together to unite (fig. 40a, b, c). The single resultant nucleolus clearly has an increased volume. By now the nucleus has very nearly attained its maximum size, with a diameter as much as five times that of the nuclei when in the primordium, almost equivalent to that of the hypobasidium.

Simultaneously the nuclear content is undergoing change. A sharp reticulum or network of threads develops throughout, highly suggestive of mitotic prophase. This increases in complexity until it reaches a stage illustrated in figure 41a. As the threads thicken, distinct, deeply staining beads representing aggregations of chromatic material are scattered throughout on them (fig. 41b). From this point on the nucleus is contracting and its entire contents become more concentrated and uniformly deeply staining. The single nucleolus gradually shifts from an eccentric to a centric position. This contraction is preliminary to a resting stage which will be followed by nuclear migration from the hypobasidium through the primordium to the epibasidium (fig. 42a, b). This contracting or post-fusion stage is the one most commonly seen; hence it probably involves a considerable span of time. With its contraction the nucleus becomes more and more homogeneous until it resumes the typical resting condition. When completely contracted the nucleus has a total volume not much in excess of the unfused nuclei at the time of migration but the nucleolar material quite evidently has been doubled in volume (see figure 71 for comparative nuclear and nucleolar ratios). The fusion nucleus ordinarily is in the center of the typical hypobasidium; in the constricted type it lies in the largest portion.

With the return to the resting condition the nucleus is ready to leave the hypobasidium. The primordial cell in the meantime has given rise to the epibasidium, more or less greatly developed. If the migrating nucleus is at all elongate the whole body moves with its long axis parallel to that of the hypobasidium, later to those of the primordium and epibasidium (fig. 43a, b, c). As in the earlier migration, there is no attenuation or change of form when the nucleus passes through the neck, for the diameter of the migrating nucleus never exceeds that of the neck. When the nucleus leaves the hypobasidium the protoplasm also withdraws, leaving the distal portion first, until the hypobasidium is completely emptied and withers. Evacuation eventually extends to the primordium and lower

portions of the epibasidium as their contents are withdrawn to augment the expanding sporogenous portion.

The epibasidial development at this time follows one of the plans already outlined. Of these the first two are by far the most common. In accord with these types, I and II, the first evidence for nuclear division is the enlargement of the nucleus followed by the appearance of threads in the heretofore homogeneous structure. This may begin at a level as early as that represented by figure 44b, but typically there are no signs of division until the nucleus comes to lie in the enlarged portion of the epibasidium, the actual sporogenous part (fig. 45a). By now all the protoplasm has withdrawn from the rest of the basidium into that region. There is seldom any further elongation or increase in diameter of the latter once division stages have been inaugurated. This first division of the secondary nucleus is taken to be meiotic. Once again the nucleus increases in volume, often nearly equalling the diameter of the tube, usually much elongated, in general conformable to the space in which it lies (figs. 46, 49). An increase in volume is the first diagnostic sign of the prophase and is the more marked because of the lighter staining properties of the nucleoplasm. This is followed by the gradual appearance of threads which soon become definitely organized. The membrane is intact about the threads and nucleolus. Chromatic beads appear on the threads but they are never as pronounced as those seen in the fusion nucleus (fig. 47). The threads thicken, become denser, and frequently are localized at a pole opposite to the nucleolus, even from the beginning (fig. 48a, b). The nucleolus is usually peripheral, rarely central. Stages represented in figure 48 may be interpreted as synaptic. Following this, the chromatic material is increasingly concentrated until it is massed more or less centrally in the nuclear cavity (fig. 48c). Slightly later, individual clumps are distinguishable in the mass and probably represent pairs or groups of chromosomes. The nucleolus, as yet distinct, from this point onwards decreases in size and finally disappears. No clear-cut evidence



was found for its direct expulsion into the cytoplasm. It usually is pushed to the edge of the nucleus quite early, and when the membrane breaks down lies free in the cavity or near by in the cytoplasm. Rarely is it distinct when the spindle is delimited; in one exceptional case a nucleolus was still quite sharp at anaphase. Commonly, what has been interpreted as a last remnant of it is seen in the cytoplasm (figs. 50b; 51a, b).

Development in accordance with type III must be considered a special case. There the prophase is distinct quite early in the development of the sporogenous portion, at times when the latter is just differentiated (fig. 45c) or even earlier. The nucleus here is less drawn out because it lies in a broader area. Aside from the earlier initiation point there is no further variation in procedure. The whole is simply a shortened basidium whose developmental processes as a consequence are likewise foreshortened.

A metaphase of the sort found in the higher plants has not been seen. As the chromatin mass separates into individual units, presumably chromosomes, a spindle is formed intranuclearly. It is always oriented parallel to the long axis, never oblique. Because of the extremely small figure, spindle fibers are not distinguishable, but the whole region appears simply as a darker-staining area. At the poles there are minute but definite dark-staining bodies, the centrosomes—more properly centrioles, for no further differentiation can be made. Their origin is unknown. Astral radiations do not occur. As the chromosomes pass into anaphase the nuclear membrane disappears, leaving the division figure in the nuclear cavity (fig. 50b, c, d, e).

At anaphase the chromosomes pass to the poles in a very irregular manner, for they may be so scattered in their distribution as to extend from equator to poles (fig. 50). It is during this scattering, if ever, that one can count the number of chromosomes present. The size of the figure and its chromosomes precludes any finality of count. As nearly as can be determined there are at least five pairs of chromosomes of different sizes.

Even though the membrane has broken down, the nuclear cavity, by virtue of its lighter staining properties, remains distinct for much longer, as figure 51c, a late anaphase, illustrates. There the spindle is stretched out and lengthened: the chromosomes are no longer discernible as individual units, for the majority are already massed together at the poles. There is no longer any trace of a nucleolus. The polar massing and the lengthening of the spindle continue until at telophase a condition represented by figure 52 is characteristic. The connective fibers or strands between the two polar masses are conspicuous. Similar persistent strands have been noted in the fungi by numerous authors. Tischler ('21-'22) designates them "karyodesmotische," Bensande ('18), "pont cinoplas-mique," and Colley ('18), "suspension fibers." That their occurrence is far from uncommon is evident from the frequency of reports covering a wide distribution of forms (cf. Blackman, '04, Colley, '18, Lindfors, '24, and Pady, '34, on rusts; Maire, '08, on divers basidiomycetes; Neuhoﬀ, '24, on the secondary nuclei of Auriculariaceae and Tremellaceae). These connections are still distinct when lighter areas around the now almost structureless chromatic masses give clear indication of the reorganizing daughter nuclei (fig. 52). Gradually a delicate membrane surrounds them. Apparently the chromatic masses prominent at telophase become the nucleoli of the daughter nuclei, a situation commented upon by Sass ('29) in his studies of Agaricaceae.

The two nuclei are usually synchronized in their behavior but now and then one matures in advance of the other (fig. 56a, b, c). A wall separating the two nuclei either is laid down before reorganization or much later. It is distinguishable at first only as a very delicate deposition, barely differentiated from the surrounding protoplasm; occasionally a clearer zone seems to mark its future position. Delay of the wall formation until the nuclei are undergoing the second division is the exception (fig. 56b). As nearly as could be determined the wall is formed by uniform deposition. Frequently a heavier aggrega-

tion is made out mid-way on the spindle strands. This may represent the initiation of the new wall (figs. 52d, 56b).

Daughter nuclei from the first division never reach a particularly high degree of reorganization, for the second division follows almost immediately. That this does ensue rapidly is inferred by the fact that early-division stages of it were never seen. Spindle orientation is longitudinal, with only an occasional and minor deviation to the oblique. Anaphases with characteristic spindles and darker-staining bodies, the chromosomes, are common (fig. 55). In figure 56a the nucleolus of one dividing nucleus has been cast aside and is disintegrating. The subsequent behavior resembles that of the first-division figures and leads to the formation of four nuclei. Moreover, the spindles are notably smaller than those of the previous division and therefore the chromosome number could not be determined with any degree of satisfaction. An exactly parallel situation has recently been recorded by Pady ('35) for the division of the fusion nucleus in the promycelium of *Hyalospora*. Ordinarily the two nuclei progress at equal rates, but when they are not synchronous the basal segment may have a nuclear phase as advanced as late telophase while the upper is still in anaphase, or vice versa (fig. 56a). Again a spindle may not have formed in one, although the second is already in anaphase. When all four nuclei are reorganized there results the typical segmented spore-bearing part (fig. 57). In that figure the mid-wall, the first one formed, is clearly older and better developed; the other two have just been laid down. As already noted, a fourth septum is exceptional, but if present it appears later at the base of the fourth segment. Figure 58a shows a true septum but figure 58b illustrates how protoplasmic remnants may simulate it.

The four daughter nuclei often display an inequality of size, that of the basal segment being subject to the greatest variation, for it is often noticeably smaller than the others. These nuclei are all in a resting condition. Though their total volume now is slightly greater than in resting nuclei elsewhere, the nucleolus is no longer enlarged. Here, if ever, two nucleoli

may appear, though apparently the condition is evanescent (fig. 59). This is in accordance with the already ascertained fact that nuclei may show variability in this respect, especially after several successive divisions, such as is the case here (Sharp, '34). That there is great variability in the nuclear and nucleolar volumes all through the cycle is evident (fig. 71).

Sterigmata promptly appear as small outgrowths from each segment (fig. 60). They are not formed synchronously nor in any regular order of succession. In most instances the fourth segment is the last to produce its sterigma, but it may be the first segment in which production is longest delayed. Initiation commonly starts in the second unit (fig. 61). There is no correlation between the position of the hypobasidium and the side of the sporogenous portion which produces the spores, but the spores are borne on the convex side. Sometimes the end segment bears its sterigma apically (fig. 63a); infrequently sterigmata may be borne on opposing sides (fig. 63d). At this time the nuclei are usually to be found directly opposite the budding sterigmata, more often peripheral than central. Gradually the sterigmata lengthen, and then small vesicles, the future spores, appear at their apices (fig. 62).

Sometimes the vesicle is preceded by a dark-staining cap or plug whose nature was not determined (fig. 64a, b). Colson ('35) finds a similar condition during early sterigmatic production in *Psalliota campestris*, where a small quantity of stainable material appears in the narrowest region. She considers it merely a mechanical retention of stain. Such would also seem to be the case here. Only the initial spore stages are hyaline, and the expanding spore is henceforth never without a definite protoplasmic content. Protoplasmic migration from the basidium segments begins early and precedes nuclear migration, which does not take place until the spore is practically mature. The latter induces striking changes in the nucleus. While the spore is forming the nucleus becomes decidedly more stainable and completely altered in shape (fig. 65a-d). Finally it becomes very dense, staining homogeneously black, and by then is quite elongate and more or less irregular in outline. It

moves into the sterigma as an undifferentiated compact mass (fig. 66a, b). Often it is long and slender during its progress into the spore (fig. 66c, d). This is not an uncommon phenomenon in the basidiomycetes. As the nuclear mass penetrates the spore the latter may show vacuolation. By now the protoplasm is well withdrawn from the segment, the last remnants passing in with, or just after, the nucleus. No protoplasmic lining ever remains in the cells as Buller ('22) noted in the *Auricularieae*. Once within the spore the nucleus undergoes corresponding changes in reverse order until the true resting nuclear state is again attained (fig. 66e, f, g, h, i). The volume is slightly under that of the antecedent resting condition.

In discussing the general morphology, the formation of exceedingly long thickened appendages in place of sterigmata was touched upon. At first it was thought that these might be indicative of direct germination as the nucleus early moved into them without undergoing change. But later it was found that they result directly from the position of the basidium and are merely a means of elevating the spores to the surface. Their consistent occurrence in regions of greater compactness in the fructification bear this out. Sometimes the lower segments of a basidium have these appendages, whereas the upper one produces an ordinary sterigma (fig. 63a). Eventually the appendages produce true sterigmata and spores, terminally. This procedure is well known in other heterobasidiomycetes; for example, in *Auricularia* the long appendages push through the gelatinous matrix to bring the sterigmata and spores to the surface. In the rusts normally (Gäumann and Dodge, *l. c.*) as well as under unfavorable conditions, the basidiospores are produced only when brought to the surface. The nuclei then move into the spores, having undergone the changes described. These nuclear changes may begin early, the initiation point being correlated with the length of the appendage (fig. 67e, f). The nuclear behavior is in complete agreement with Neuhoﬀ's criterion for a sterigma. Linder speaks of variation in sterigmatic length in *H. intermedia* (see his pl. 41, figs. 13-15), a situation which is probably tantamount to the one just described.

Germination, which may take place at once, begins with the emission of a short germ tube and a sterigma upon which a secondary spore exactly like the first is borne (fig. 68b, c, d). This is the so-called "germination by repetition," long a recognized character of the heterobasidiomycetes (Patouillard, '87). Not only is the morphology of the sterigma the same but the nucleus, in order to pass into the secondary spore, is altered in exactly the same fashion as characterizes the passage from basidial segment to spore (fig. 69). Nuclear division within the spore has never been seen. At times spores begin germinating while still attached to the sterigmata (fig. 68b). No data pertaining to the actual spore discharge were obtained.

Attempts to culture *H. Lagerheimi* have been unsuccessful so far. Unfortunately no fresh material was available, and herbarium specimens of the 1934 collections had to be relied upon. Spores from that source sown in hanging-drop cultures of sterile distilled water gave a goodly percentage of germination within from 24 to 48 hours, but transfers were never successful. From observation of spore behavior in the hanging-drop cultures it is readily seen that the usual mode of germination is by repetition. Möller illustrates septate spores, each segment of which is capable of producing a secondary spore. This has not been seen. Although in Patouillard's type material a spore with two germ tubes was found, septation between was indistinct. The spores do occasionally segment in germination, but their subsequent behavior was not determined. Small sub-globose conidia appear in older cultures. Their mode of origin was not seen. Frequently they are massed, just as Möller reported.

Before the appearance of the germ tubes the spores are quite hyaline, in most cases with a single, rather conspicuous oil globule. As germination processes are initiated this divides into two to many with corresponding reduction in size. When the germ tube arises the contents of the spores are distinctly granular with numerous oil bodies. The tubes themselves are mostly lateral, but may be terminal, in position. At their apices a small bubble-like protuberance is the first sign of the

secondary spore. This remains quite hyaline until maturity when the content of the original spore is discharged into it. In some cultures within a few days delicate mycelial outgrowths were evident (fig. 70).

### TAXONOMIC CONSIDERATIONS

All the species of *Helicogloea* are entirely saprobic. They are found on well-decayed woods of various kinds, including pine, alder, birch, beech, oak, aspen, poplar, and willow, rarely on humus or soil. One species occurs on grasses from whence it takes its name, *H. graminicola*. Collections have been made of some species practically throughout the year; others seem to have more seasonal limitations. Any is more likely to be found in damp rather than dry weather. Geographically, the distribution is scattered. *H. Lagerheimi* is the most widespread. Besides the type locality, Ecuador, it has been reported from France, England, and the United States. The only other North American species are *H. caroliniana*, as yet found only in the type locality, North Carolina, and *H. pinicola* recently reported from Canada.

As pointed out earlier, the chief considerations of the genus have been taxonomic. The most comprehensive treatment is that of Bourdot and Galzin. They characterize the genus as "floccose or gelatinous-mucous, spreading; the probasidium in the form of a sac, laterally pendent and giving rise to a basidium with three transverse walls; sterigmata lateral (one terminal); spores hyaline, smooth." By reason of the floccose or gelatinous nature of the parent genus, these authors have erected the subgenus *Saccogloea* to care for the mucose-gelatinous forms. Furthermore, they comment: "The French species of *Saccoblastia* do not always show the generic characters clearly; the contents of certain probasidia appear often to be a reserve utilized for the formation of the basidium, but it seems in many cases that it is the probasidium itself which becomes erect and is directly transformed into a basidium. At least, the section shows often all the intermediate stages between the probasidium as a pendent sac and the curved or erect

basidium." In view of such indefiniteness all obtainable species were studied. A brief description is given of each, chiefly for its morphology.

*HELICOGLOEA pinicola* (Bourd. & Galz.), comb. nov.

Pl. 13, figs. 72a-l, 73a-c.

*Saccoblastia pinicola* Bourdot & Galzin, Soc. Myc. Fr.

Bull. 25: 16. 1909.

The type has not been seen, but two collections of Galzin's, and Bisby's Canadian gathering were examined. They are all truly floccose. The scattered receptacles of Galzin's collections are Cartridge-Buff.<sup>2</sup> A few patches here and there, gelatinous in consistency, are a deeper color—Olive-Buff to Deep Olive-Buff. The Canadian material shows no gelatinous areas.

This species is clearly a member of the floccose section. Bourdot's and Galzin's description answers with some exceptions. The hypobasidium was found to be consistently larger than the range given by these authors. They say it is  $40-45 \times 8-12 \mu$ ; measures made here extend the range to  $19-56 \times 7-14 \mu$ , the majority in Galzin's material falling around  $50 \mu$  in length. The morphological plan is even less in agreement. Bourdot and Galzin refer to variation in the "basidia" but not to any in the hypobasidia. In the material studied the latter is extremely noticeable. Irregularities most frequently take the form of forked or branching hypobasidia (fig. 72a, i, j). Forked basidia mentioned and figured by Bourdot and Galzin have not been found, but figure 72i, for example, strongly suggests that these authors may have mistaken forked hypobasidia for forked basidia. The most striking feature is the mode of origin of the basidium parts. Occasionally the primordium is a terminal cell of varying length, as in *H. Lagerheimi*, but usually it is intercalary. The hypobasidium arises in the usual way as a lateral outgrowth but at maturity presents a great variety of forms—from straight to constricted to forked (fig. 72). The size is usually great in comparison with those of other species. The epibasidium is produced as a lateral

<sup>2</sup> Capitalized color names are from Ridgway, R., Color Standards and Color Nomenclature. 1912.



out-pushing of the primordium at or near its apex. Hence one commonly finds the basidia appearing in chains in contrast to the type of proliferation common in *H. Lagerheimi* (fig. 73e). At maturity the spore-bearing region of the epibasidium is three- or four-septate, and the portion posterior to it withers. Apical germination of the terminal segment is common (fig. 72e, k).

Bourdot and Galzin say this species is "very close to *H. graminicola*, of which it is perhaps only a variety. It differs in habit and the basidia and spores are notably larger." There seems to be little basis for the assumption of varietal status. True, both species have conspicuous clamp connections and both are supposedly floccose, but the epibasidial character and origin in the two are entirely different, nor does *H. graminicola* ever show the hypobasidial irregularities so marked in *H. pinicola*.

A collection from Litschauer of this species on *Alnus viridis* undoubtedly belongs to the form *alniviridis*, although it was approved by Bourdot before he segregated the form. It shows no deviation from described characters except that there was no paucity of hypobasidia such as Bourdot reported. Morphologically it is identical with the species (fig. 73 a-e). The validity of forms founded on substratal attachment is questionable for pure saprobes, even more so in this case since the advent of Bisby's specimen which was found on *Populus*. It, too, showed no specific differences.

FRANCE: Causse Noir, April 25, 1910, *Galzin*, 20555 (in Herb. Univ. N. Car. ex Herb. Bourdot); Nov. 19, 1916, *Galzin*, 2104 (in Farlow Herb. ex Herb. Burt).

AUSTRIA: Tirol, Aug. 15, 1924, *Litschauer* (in Herb. Univ. Iowa).

CANADA: Manitoba, Victoria Beach, Aug. 23, 1935, *Bisby*, F5635.

*HELICOGLOEA graminicola* (Bres.), comb. nov.

Pl. 13, figs. 74a-d.

*Saccoblastia graminicola* Bresadola, Ann. Myc. 1: 112.  
1903.

After this is moistened it appears as a thin gelatinous coating on a grass stem, in color Vinaceous-Buff. There is nothing in its structure or consistency to justify Bresadola's

adjective "tomentose." From phloxine-stained mounts one can readily distinguish its salient characters. Micro-dimensions show close correspondence to those given by Bresadola. The primordium is terminal and it gives rise to the epibasidium. A conspicuously elongate connection between primordium and sporogenous portion is not found. The hypobasidia are large, coarser in appearance than those of *H. Lagerheimi*, more constant in size than those of *H. pinicola*, and are never forked. All the protoplasm withdraws from the hypobasidium but not necessarily from the primordium, which may still show a definite protoplasmic content after the segmentation of the spore-bearing region (fig. 74c). Clamp connections are prominent on the hyphae, sometimes appearing on the basal septum of the primordium which just beyond on the opposite side is producing the hypobasidium (fig. 74a).

*Eichler* (in Farlow Herb. ex Herb. Bresadola, ex Herb. Patouillard).

*HELICOGLOEA intermedia* (Linder), comb. nov.

Pl. 13, figs. 75a-h.

*Saccoblastia intermedia* Linder, Ann. Mo. Bot. Gard.  
16: 488. 1929.

A slide of the type material prepared by Linder was studied for the morphology of the species. From this it was clear that the origin of the saccate hypobasidium is intercalary, not terminal, or only exceptionally so. Following nuclear fusion within the hypobasidium, the latter germinates proximally to the epibasidium. After great elongation four sterigmata and spores are formed on the thickened end. Linder uses the terms "probasidium, promycelium, and basidium" for these parts. However, there is no reason, in spite of morphological variation, why Neuhoff's terminology is not applicable. The clavate type simply represents direct development from a terminal primordium. In this event, when a lateral sac is not produced, fusion takes place in the clavate portion itself; hence it is to be interpreted as the hypobasidium and its subsequent outgrowth as the epibasidium. Figure 75 is included merely for comparison with the other species.

Linder speaks of the saccate hypobasidium exhibiting distal germination at times. If his figures (pl. 40, fig. 4; pl. 41, fig. 9) represent the best evidence for that phenomenon, its occurrence is questionable. Succeeding stages would be convincing but none was found. However, the hypobasidia are frequently constricted, once or more, and it is possible that this so-called distal germination is only an extreme constriction. Distal germination was never seen in *H. Lagerheimi*. Hypobasidia of the form illustrated in figure 75e, *H. intermedia*, might be interpreted as unusually constricted, especially when compared with figure 18f and g of *H. Lagerheimi* which is so construed. Furthermore, if the orientation of the two fructifications is the same, then distal germination could only occur for those rare cases where the hypobasidia are lateral or pendent.

CUBA: Soledad, Sept., 1924, *Linder*, TYPE (in Herb. Mo. Bot. Gard.).

**HELICOGLOEA caroliniana** (Coker), comb. nov.

Pl. 13, figs. 76a-c.

*Saccoblastia caroliniana* Coker, Jour. Elisha Mitchell Sci. Soc. 43: 233. 1928; *S. ovispora* Möller var. *caroliniana* Coker, Jour. Elisha Mitchell Sci. Soc. 35: 121. 1920.

Coker's descriptions are so adequate that little need be said here. The fructification is a particularly well-developed gelatinous one. In its morphological behavior it resembles *H. Lagerheimi* very closely. A series of diagrams is included for comparison. Here, as in the other species of the genus, long appendages may precede the formation of sterigmata and spores (fig. 76d).

NORTH CAROLINA: Chapel Hill, April 15, 1920, *Couch*, 4256 (in Herb. Univ. N. Car.); Chapel Hill, July 31, 1920, *Couch*, 4601 (in Herb. Univ. N. Car.).

**HELICOGLOEA LAGERHEIMI** Patouillard, Soc. Myc. Fr. Bull. 8: 121. 1892. Pls. 7-12; pl. 13, figs. 77-78; pl. 14.

*Saccoblastia ovispora* Möller, Protobasidiomyceten, Bot. Mitt. 8: 16. 1895.

*Saccoblastia sebacea* Bourdot & Galzin, Soc. Myc. Fr. Bull. 25: 15. 1909.

*Saccoblastia sebacea* var. *vulgaris* Bourdot & Galzin,  
Hym. de France, p. 5. 1928.

*Saccoblastia sebacea* var. *pruinosa* Bourdot & Galzin,  
Hym. de France, p. 5, 1928.

A study of the type material resulted in the above changes in synonymy. Figures 79–81 show the development of the basidium as seen in Patouillard's material, from the initiation of the primordium to the mature basidium and spores. Though micro-dimensions are consistently larger than those from the majority of collections, they do not exceed the uppermost figures obtained. There is no uncertainty about the identity of this material with Möller's or Bourdot's and Galzin's. Therefore the earliest name takes precedence. On the basis of basidium size *H. caroliniana* is perhaps the nearest species. But the two are so totally different in their habit they could never be confused. In particular, the hypobasidia of the type collection are sometimes constricted and frequently are set farther forward in relation to the basal wall of the primordium (fig. 79d) than usual. No case of intercalary origin was noted in this material.

*Saccoblastia sebacea* B. & G., an acknowledged gelatinous form, has been separated from *S. ovispora* Möller largely because the latter was supposedly floccose or hypochnoid. A study of all available specimens and descriptions has been made in an effort to straighten out the situation.

Of *Helicogloea Lagerheimi* (*Saccoblastia ovispora* Möll.), Möller wrote: "Sie bildete einen dünnen, fast durchsichtigen lockeren weissen Ueberzug, der in ganz unregelmässiger Umgrenzung mehrere Centimeter in jeder Richtung sich ausdehnte. Bei sehr feuchtem Wetter sieht dieser Ueberzug fast schleimig aus, da das Gewirr der Fäden Wasser zwischen sich festhält, bei trocknerem Wetter dagegen bemerkt man nur einen lockeren Hyphenfilz, der bei vollständigem Trocknen zur Unsichtbarkeit zusammenfällt." (l. c.). Ferry ('96) the following year translated Möller's work into French, in addition utilizing Möller's plates. The structure of the fructification is described as irregular patches of white loosely interwoven hyphae. Lindau ('97) introduced the adjective "wer-

gartig" in his characterization. As yet only Möller's species were known. Patouillard ('00) delineated the genus *Saccoblastia* as floccose, soft, and said of the tribe Septobasidiés to which he assigned it: "Floconneux ou crustacé, non gélatineux." Chronologically Bresadola's ('03) report is next, which described *H. graminicola* as "tomentose." Clements ('09) placed the genus (as *Saccoblastia*) in that group of Auriculariae having a byssoid pileus. Clements and Shear ('31) adhere to this characterization. Saccardo ('82) qualified the structure by saying, "Est quasi *Hypochnus* sporis pleurogenis." Killerman ('28) repeated Lindau's diagnosis for two species, having replaced *H. sphaerospora* with *H. graminicola*. The character of floccose as opposed to gelatinous is the distinguishing one for two sub-genera in Bourdot and Galzin.

Thus there had gradually crept into the literature the conception of floccose or hypochneid fructifications in *Helicogloea*. *H. pinicola* is truly floccose. The interpretation of *H. Lagerheimi* as floccose probably has been considerably strengthened by Bresadola's comment to Coker in reference to *H. caroliniana* which was first described as a variety of *H. Lagerheimi*. Coker says (*l. c.*): "I later sent some to Bresadola who has described a sp. of *Saccoblastia* and seems to have seen *S. ovispora*. He writes as follows: 'For me it is a species quite distinct from *S. ovispora*. The genus *Saccoblastia* is not gelatinous; your species is gelatinous like *Platygloea*; . . .'"

An exactly parallel situation has arisen in the case of *Stypella minor* Möller and *Tremella gangliiformis* Linder. As Martin ('34) points out, the error is not in Möller's original description but in subsequent misplaced emphasis and consequent distortion. Since the type of *Helicogloea Lagerheimi* is mucous-gelatinous, all necessity of maintaining these species separately is removed. Unfortunately, Möller's type specimen has not been located; Rick's material, agreeing well with Möller's descriptions and coming from an adjacent province, gives strong likelihood of being the same fungus. The type of Bourdot's and Galzin's species likewise has not been seen, but all the collections so labelled which have been at

hand were decidedly not floccose. When any of these specimens is moistened it is mucous-gelatinous, but as it dries one can trace just such a sequence as Möller described.

Throughout the genus there seems to be not only inconsistency of interpretation but a real variation in the nature of the fructification itself. Wakefield and Pearson ('23) note of *H. Lagerheimi* that a series of specimens shows the "mucous-gelatinous" texture only in later stages. "When at its best the fungus has somewhat the consistency of *Corticium confluens*, and is beautifully pruinose with the projecting basidia and spores." Rick (personal correspondence, 1934) says: "The *Saccoblastias* are surely hypochnoid without true hymenium, but when well developed they are gelatinous, like *Exidiopsis*, and dry a little glancing." To Rick obviously hypochnoid connotes structure rather than consistency. On that basis all the species are "hypochnoid." It is significant that he considers the genus gelatinous, even though earlier he had been in accord with conventional treatments when in a monograph of protobasidiomycetes ('33) he referred the genus to the floccose Auriculariales. As already remarked, *H. pinicola*, which is distinctly tomentose for the most part, has some scattered gelatinous patches.

Möller's statements may have left latitude for differing interpretations, but his figures are clear-cut and easily show the close resemblance to *H. Lagerheimi*. A table of measurements for the specimens under discussion shows there is no reason to maintain any as distinct species because of variation in size. Only in the event that Möller's type proved to be distinctly floccose would it be reasonable to retain that species.

Two collections from Brazil were studied, both Rick's. The first of these was quite inconspicuous until moistened, when it became visible as thin gelatinous film, faintly pustular, of a Buffy-Brown color; no part of it could be interpreted as floccose. Unfortunately, the specimen was so contaminated with hyphomycetes that mounts were far from satisfactory, the more so as it did not seem to be in a particularly advanced fruiting condition. However, all evidences indicated a struc-

tural development much like the type of *H. Lagerheimi*. The mycelium is typical; oblong-ovoid hypobasidia—straight or constricted—are borne laterally on terminal primordia (fig. 78a). There is rarely deviation from the typical epibasidial production (fig. 78e).

The second of the collections may easily be a portion of the first, to judge from appearances. Certainly when examined before moistening it is not at all floccose. If discernible at all when dry it is only as a dried mucoid layer spread thinly on the bark substratum. As it revives in a moist-chamber it quickly swells into a mucous-gelatinous layer, exactly like that of the first collection. This material offered a greater range of basidia, though mature ones were scarce. Very infrequently basidia of intercalary origin were found. The hypobasidia are often constricted. Figure 78 a-g outlines the structural plan for both collections.

Examination of the other herbarium specimens suggested emphasis of the following points. Usually the primordium of the basidium is of terminal origin, rarely it is intercalary. The hypobasidia are straight or constricted, but in a few collections irregular ones approaching the *H. pinicola* type occur. Micro-dimensions show a greater range than those given by Bourdot and Galzin, but they are fairly consistent for the particular collection. All the fructifications are decidedly gelatinous with a color range from Ochraceous-Buff to Fuscous, most commonly Grayish-Olive.

Bourdot and Galzin have included several varieties. Opportunity to examine a large number of collections of the species and the varieties *pruinosa* and *vulgaris* from Bourdot's herbarium showed that the varietal segregates are untenable on both habital and structural bases. According to Bourdot and Galzin, the variety *vulgaris* differs only in that it is "thinly spread in large gelatinous patches." When moistened it so appears; its color is pallid Cinnamon-Buff or Grayish-Olive. There is scarcely anything distinctive about this; certainly in structure it is identical with the parent species as shown by figure 77.

The variety *pruinosa* is segregated by these same authors on the bases of micro-dimensions and growth form. The measures of the hypobasidia in the material examined slightly exceed those cited by Bourdot and Galzin. Spore size extends from  $8-11.5 \times 5-6.5 \mu$ . Though the spore size of the parent species ranges from  $8-18 \times 4-9 \mu$ , the majority fall in a middle grouping around  $9-11 \times 5-7 \mu$ . It would be impossible to make a separation on spore size. The micro-dimensions do not distinguish the variety from the parent species; morphologically there is no difference between the two, and the color range is also closely parallel. No illustrations are included.

From the table following it is clear that there is more reason to set aside separate varieties than to maintain the former species because of differences in measurements. Such a criterion is hardly reliable in a group as variable as the heterobasidiomycetes.

*HELICOGLOEA LAGERHEIMI* PAT.

	Hyphae	Hypobasidium "sac"	Epibasidium	Spores
Type	2-6 $\mu$	18-38 $\times$ 5.5-10 $\mu$	69-100 $\times$ 5-7.5 $\mu$	13-15-18 $\times$ 6.5-8 $\mu$
Möller's measures	2-6 $\mu$	30 $\times$ 8 $\mu$	100 $\mu$	13 $\times$ 7-9 $\mu$
Rick's colls.	2-6 $\mu$	18-33 $\times$ 6-7.5 $\mu$	65 $\times$ 4.5 $\mu$	15-18 $\times$ 6-7.5 $\mu$
B.'s & G.'s measures	2-6 $\mu$	18-30 $\times$ 6-9 $\mu$	45-75 $\times$ 4-6.9 $\mu$	8-10-15 $\times$ 5-6-8 $\mu$
Other specimens	2-6 $\mu$	15-39 $\times$ 5-13 $\mu$	58-105 $\times$ 5-9 $\mu$	8-12-17 $\times$ 4-9 $\mu$
var. <i>vulgaris</i>	2-6 $\mu$	18-28 $\times$ 5-8 $\mu$	50-60 $\times$ 5-6 $\mu$	9-11 $\times$ 6-7 $\mu$
var. <i>pruinosa</i>	2-6 $\mu$	16-32 $\times$ 5-9.5 $\mu$	50-60 $\times$ 5-6 $\mu$	8-11.5 $\times$ 5-6.5 $\mu$
Roger's meas- ures	3-4.5-6 $\mu$	16-32 $\times$ 7-10 $\mu$	75-100 $\times$ 4.5-7.5 $\mu$	11-14.5 $\times$ 5-7.5 $\mu$
Total range	2-6 $\mu$	15-39 $\times$ 5-13 $\mu$	45-105 $\times$ 4-9 $\mu$	8-18 $\times$ 4-9 $\mu$

ECUADOR: Chorrera de Agoyan near Baños, Jan. 1892, *Lagerheim*, TYPE (in Farlow Herb. ex Herb. Patouillard).

BRAZIL: Rio Grande do Sul, São Leopoldo, 1931, *Eick* (in Farlow Herb.); 1931, *Eick* (in Herb. Mo. Bot. Gard.).

UNITED STATES: Iowa, Iowa City, Oct. 5, 1932, *Rogers*, 242; July 8, 1934, *Rogers*,



305, 306; July 9, 1934, *Rogers*, 274; Missouri, Springfield, Oct. 2, 1933, *Looney* (all in Herb. Univ. Iowa).

FRANCE: Allier, *Bourdöt*, 5750 (in Farlow Herb. ex Herb. Patouillard); *Bourdöt*, 5750, 5382, 39135 (in Herb. Paris ex Herb. *Bourdöt*); Aveyron, *Galsin*, 3895, 3951, 4334, 5749, 7856, 7961, 10085, 11982, 13816, 13817, 14003, 14247, 14270, 14368, 14411, 14606, 14764, 14790, 14800, 14825, 14828, 16605, 16632, 16638, 16641, 16646, 16647, 16704, 16933, 17210, 17454, 18828, 18899, 19067, 20134, 21132, 23717, 23718, 23719 (in Herb. Paris, 23305, 6017, 6508, 7612, . . . , 23288, 23289, 23240, 12151, 12153, 12349, 12351, 12350, 23291, 23308, 23333, 23293, 12348, 12411, 23294, 23295, 23302, 23297, 23296, 23300, 23303, 23301, 23304, 23298, 23335, 14915, 15419, 15479, 15991, 18561, . . . , 24120, 24121, 24122); St. Guiröl, May 6, 1910, *Galsin*, 5815 (in Herb. Paris, 23287 ex Herb. *Bourdöt*); Tarn, July 23, 1909, *Galsin*, 4316 (in Herb. Paris, 23306 ex Herb. *Bourdöt*); April 10, 1916, *Galsin*, 19561 (in Herb. Paris, 2331 ex Herb. *Bourdöt*); St. Priest-en-Murat, Nov. 1914, *Bourdöt*, 42362 (in Herb. Univ. N. Car. ex Herb. *Bourdöt*); Orne, Oct. 1925, *E. Gülburt*, 1313 (in Herb. Paris, 39816 ex Herb. *Bourdöt*).

ENGLAND: London, Feb. 1922, *Pearson* (in Herb. Paris ex Herb. *Bourdöt*).

## DISCUSSION

Mitotic processes of *Helicogloea* give no indications of abnormalities, although a few stages encountered need some exposition. The unusual spindle disposition in nuclear division is by no means restricted to this form. Kniep ('13) noted a similar irregularity in *Hypochnus terrestris*. His figures include a definitely crossed type and one slightly angled, both from a germ tube; and the usual conjugate type from the mycelium. This gradation is comparable to that found in the terminal hyphal cells of *Helicogloea*. Tischler (*l. c.*) adopted Kniep's figures; neither author offers an explanation. Neu-hoff ('24), throughout his studies on Auriculariaceae and Tremellaceae, saw mitosis only once—in *Achroomyces Tiliae*. Quite obviously, his illustration denotes that the spindles were crossed, but of this he makes no mention. However, he regards as abnormal crossed spindles in the hypobasidial division in *Exidia pithya*. This same phenomenon has been demonstrated frequently in the divisions of the fusion nucleus and in one instance of nuclear division in the spore (cf. Rogers, '32; Lander, '35; Colson, '35). That the clamp connection is a device to permit the side-by-side orientation of the spindles for the conjugate division of the dikaryon and a means to bring non-sister nuclei together, is widely accepted. Since there are

no clamp connections in this species, it is perhaps reasonable to assume that the crossing of the spindles is imposed by the narrow limits of the cell diameter.

Sass ('29) has commented upon the fact that apparently the chromatin masses at telophase become the nucleoli of the daughter nuclei. This is quite evidently so in the meiotic divisions of *Helicogloea* where a complete sequence can be traced easily from late anaphase to the reorganizing daughter nuclei, still joined by the drawn-out spindle threads. To explain this it is necessary to assume that the true nucleolus is distinct from this chromatic mass. This, then, would be in line with the second of the explanations offered by Sass for variation in chromosome and reticulum behavior among the several species that he was studying. In support of this hypothesis, that the chromatin is localized or stored in the large "nucleolus-like body" which therefore is to be considered a karyosome from which the chromatin passes into the achromatic framework during pre-meiotic processes, he presents four lines of evidence. Nuclei of *Helicogloea* are too small to permit confirmation. Sass's final statement, that the true nucleolus is a minute body expelled from the chromatin body just before spindle formation, offers a clue to what is evident in *Helicogloea*. As figures 45, 48 (cf. earlier stages also) show, there is a decided decrease in nucleolar size during prophasic periods evident from the first, and after the spindle and chromosomes are definitely formed a minute body is still visible, often some distance removed from the spindle. Later it too disappears. Though this cannot be conclusive without tracing the origin of the reticulum and chromosomes, nevertheless the behavior is suggestive. It seems to occur commonly in many fungi; Wakayama ('30) has promoted similar ideas based on observations of *Aspergillus*.

One of the most curious and striking of aberrations concerns the chromosomes in their passage to the poles. This consistently is irregular, so that from metaphase through anaphase they are scattered from equator to pole, sometimes more or less clumped together. Throughout the literature

this condition is commonly figured (cf. Juel, '98; Ruhland, '01; Kniep, '13; Colley, '18; Bagchee, '25; Wakayama, '30, '30a, '31, '32) not only for basidiomycetes but for ascomycetes as well. Wakayama's extensive works, especially on Agaricaceae, show that this phenomenon is more characteristically present than a regular separation of the chromosomes. His comment that this scattering is due to very different migration velocities for each univalent is the only stated attempt noted in elucidation of the point. He furthermore remarks that in spite of this unusual procedure it nowise follows that the nuclear process is not typical.

Even more striking than this is the behavior of the nuclei in their migration from the parent cells or accessory appendages into the spores. Their extreme chromaticity, attenuation, and loss of form mark the narrow constricted portion through which they must pass just prior to entering the spore as a true sterigma, *sensu* Neuhoff. Such nuclear alteration has been remarked time and time again in the basidiomycetes. Maire ('02) noted that in the heterobasidiomycetes the nucleus passed into the germ tube without change but in moving into the spore through the sterigma it became constricted. It remained for Neuhoff, however, to crystallize the phenomenon into a definite criterion. According to his dictum, cytological in its foundation, a migrating nucleus in passing through a sterigma into a spore assumes just such an elongated form, at the same time giving a chromatin stain reaction. It is tenable then that the long inflated appendages so frequently developed in place of the shorter subulate sterigmata are accessory. This is strengthened still more by the fact that when they reach the surface or a position favorable to spore discharge true sterigmata are formed and the nuclei go through them into the spores in the changed form. That such attenuation is not the result of mechanical constriction due to the size of the sterigma is upheld by the initiation of the condition long before the nucleus reaches that portion of the sterigma (cf. Whelden, '34, on *Tremella*). Spore germination processes are initiated by the production from the primary spore of filaments of varying

length. This in turn develops a true sterigma through which the nucleus moves into the secondary spore, having previously undergone precisely these specified changes. The sterigmata in relation to the spores by all evidence fit Buller's ('22) functional criteria, viz., that "the typical sterigma . . . is . . . an organ for the violent discharge of the spores." The hilum region of the *Helicogloea* spore is well developed. Observation of the actual mechanism of discharge was impossible without fresh material.

A lack of consistency in the terminology employed for the basidiomycetes and the interpretation of their diagnostic structure, the basidium, has long marked the literature, the situation only recently becoming clarified and more constant as careful morphological and cytological studies have brought out true and natural relationships. *Helicogloea* is classified with those basidiomycetes which have transversely septate basidia as opposed to those in which the basidia are vertically divided or those which remain undivided. Historically, the basidiomycetes have been separated into various subdivisions on the basis of basidium morphology, e. g., Hyménomycètes-Hétérobasidiés and Homobasidiés (Patouillard, '87); Proto- and Autobasidiomycetes (Brefeld, '88); and Acrosporeae and Pleurosporeae (van Tieghem, '93). As Gäumann and Dodge (*l. c.*) point out, the first two complements carry a phylogenetic implication and the last is neutral in its connotation. These categories do not comprise identical groups. Van Tieghem considered septum formation an accessory character, the fundamental one for him being the mode of spore insertion, expressed by his terms Acrosporeae and Pleurosporeae. These primary divisions each included both septate and non-septate basidia, which he spoke of as Phragmo- and Holobasidia. Patouillard's groupings have a less artificial basis. Furthermore, he recognized in distinguishing between hetero- and homobasidial groups that the spores of the former usually germinate by the production of secondary spores, whereas those of the latter germinate by mycelia. Such a distinction is a more reliable criterion for primary segregation of the ba-

sidiomycetes than the character of septation. In recent years the use of the terms heterobasidiomycetes and homobasidiomycetes has found acceptance. The heterobasidiomycetes include those forms with secondary spore germination and basidia usually divided in some fashion—the notable exception being the undivided basidia found in the Dacrymycetaceae.

At its earliest inception the basidium of *Helicogloea*, or that of almost any heterobasidiomycete, is not distinguishable from one of a homobasidiomycete at a comparable level of development. Both are usually single, terminal hyphal cells containing a pair of nuclei, descendants of the dikaryon of the sub-terminal cell. From this point onwards the resemblance is diminished in a greater or lesser degree. The true homobasidium remains undivided and develops no accessory parts. Therefore it functions both as zeugite and gonotocont. Variation in some of the heterobasidiomycetes is founded on the separation of these critical stages and consequent modification of morphological patterns.

In *Helicogloea* the initial cell of the basidium complex has been designated as the primordium, a term not inappropriate for the same stage of the homobasidium. From here on the similarity ceases. The subsequent development in the heterobasidiomycetes, and in particular in the genus under discussion, involves the production of distinct and often persistent morphological entities. For *Helicogloea* these take the form of the "sac" and of spore-producing out-growths. Möller called the former "tragzelle," thus merely indicating its position and form with no intimation of its cytological significance. Van Tieghem's terms—probasidium and basidium—have been more widely adopted by later workers. Their connotation does not permit the probasidium as part of the basidium proper and hence introduces a misleading idea of their true relation to the nuclear functions. For this reason they are rejected here. Probasidium, promycelium, and basidium have also been applied to the different parts of the basidium, especially by those who were particularly impressed by the striking resemblances of the group to certain Uredinales.

These terms are rejected on the same basis as the preceding ones.

A cytological interpretation is credited to Wettstein ('11), who emphasized the fact that in the basidium the fusion of two nuclei takes place before the formation of the spores. As Rogers ('34) has stated, the most satisfactory concept of the basidium—for both homo- and hetero-types—is Neuhoﬀ's (*l. c.*). It is basically cytologic, for he considers the morphological development consequent upon that. According to that author, the mature basidium of the heterobasidiomycetes is composed of a *hypobasidium* which has "germinated" to one or more appendages, the *epibasidia*. This terminology allows adequately for any morphological separation of karyogamy and meiosis. If both these critical events take place in the hypobasidium several epibasidia result, usually four, sometimes eight, consequent upon the number of nuclei produced—as in the Tremellaceae and Tulasnellaceae, respectively; if meiosis is delayed until after germination there is produced, naturally, only one epibasidium. In the latter category are placed the Auriculariaceae, and, among them, *Helicogloea*.

It is a simple matter to reconcile the situation in that genus with this conception. Neuhoﬀ defines the hypobasidium as the "lower, commonly inflated vesicular part of the basidium"; the epibasidium as the "upper, more uniformly tubular part of the basidium." The two parts are in the majority of instances in free communication at all times. If this ground-plan is applied to the behavior in *Helicogloea* all the species resolve neatly into that scheme. That is, the "sac," a lateral expansion of the primordium, is the place where the two nuclei come together and fuse, and therefore it is truly hypobasidial. From the primordium is produced apically a single appendage in which the secondary nucleus undergoes meiosis, the whole eventually elongating and bearing sterigmata and spores. This quite properly is the epibasidium. The two parts are never separated but are at all times in open communication. Even for those species in which the primordium is intercalary this holds. It is evident then that there is nothing in Neuhoﬀ's

criteria to exclude their general application to *Helicogloea*. At first there may seem to be a morphological discrepancy which would prevent their literal adoption. Apparently only those forms with direct germination of the primordium without an accessory part—and the clavate hypobasidium of *H. intermedia* is the only one which answers that description—seem to be completely in harmony with Neuhoﬀ's principles. However, it is only necessary to include for the others the primordial portion as part of the hypobasidium, which therefore is to be described as a hypobasidium with a lateral expansion. In the light of this interpretation the production of the epibasidium is seen to be from the hypobasidium, whatever the constitution of the latter (cf. *H. pinicola*, *H. intermedia*, and *H. Lagerheimi*).

There is good morphological justification for this. The primordium and sac are plainly complementary parts of one structure, and the epibasidium, an outgrowth from either part, is filled with protoplasm at their expense. For reasons of convenience the term primordium is retained to cover the primary phase of the hypobasidium; likewise, the accessory development where karyogamy occurs is referred to as the hypobasidium and in formation is secondary. This is the only example so far known in which there is such an obvious morphological separation of the initial portion of the hypobasidium from that in which karyogamy occurs. One minor deviation from Neuhoﬀ's nuclear scheme must be noted. The secondary nuclei of those Auriculariaceae which he investigated characteristically began migration into the epibasidium during the post-synaptic stage of the first meiotic division. In *Helicogloea* the fusion nucleus contracts to a typical resting condition and then migrates into the epibasidium where it undergoes meiosis. In other words, not only is the hypobasidium divided into two distinct units, a condition not known in other Auriculariaceae, but the nuclear cycle is interrupted by a resting stage—even though it is so short it clearly is only to allow for migration.

The hypobasidium of *Helicogloea* has often been interpreted as a storage organ, an ecological view which Möller inaugu-

rated. His statement that the contents of the hypobasidium would be withdrawn completely and migrate into the developing epibasidium was based on accurate observation, it is true. The idea of a storage organ, unique for this genus, was again expressed by Gäumann ('22). But obviously the time relation between fusion and migration of the secondary nucleus (it contracts and rests only long enough to orient itself for emigration) precludes such an interpretation. One must admit, though, that by virtue of this behavior there is introduced the potentiality for a longer resting period. That the hypobasidium is not a storage organ, in which reserves are held in readiness to produce the epibasidium when favorable conditions so permit, is further substantiated by the observation that as often as not epibasidial germination and elongation occur without any visible augmentation from the hypobasidium. The complementary parts of the hypobasidium are to be construed, then, only in the light of the nuclear cycle.

Within the genus itself there is manifested in basidial characters a progressive sequence from simpler to more advanced forms. Quite obviously, the least developed type would be the clavate form of *Helicogloea intermedia*. The basidium arises as a terminal primordium, becomes swollen to accommodate karyogamy, and then germinates directly to the epibasidium. Here, then, is the simplest type of hypobasidium found in the group, for it consists of only one morphological entity. It is significant that, according to Linder's notations, this type of hypobasidium is the first produced. Since there is a saccate type of hypobasidium in the same species, the production of the clavate type takes on a vestigial aspect. Rogers ('34), going on the assumption that the "primitive auriculariaceous basidium is one with a persistent hypobasidium, clearly distinguishable in all stages," uses as an example the saccate *Helicogloea* hypobasidium showing distal germination. Such behavior is decidedly atypical if it occurs at all. The clavate form is much more acceptable as the primitive type of auriculariaceous basidium, for its hypobasidium is a sharply delimited, persistent organ. Second, there may be placed the



type characteristic of the majority of species, *H. Lagerheimi*, *H. graminicola*, and *H. caroliniana*, whose basidial primordia likewise are terminal, but which give rise to a secondary part, morphologically distinct. Advance is also indicated by the fact that the clavate type shows no adjustment for proliferation, whereas in the second type there is ample allowance through the subterminal cell development. The remaining species are all marked by this division of the hypobasidium into primary and secondary portions. *H. pinicola* shows an entirely new departure in the intercalary origin of the basidium. But nevertheless the primary portion of the hypobasidium remains the source of germination. (Note that infrequently this pattern is found in the preceding species, too). In the saccate type of *H. intermedia* it is the secondary portion of the hypobasidium which germinates. This possibly represents the highest level, for it suggests a potentiality for a resting stage, and, through encystment, eventual separation. In all types meiosis occurs in the epibasidium.

It is evident that the hypobasidium, and in particular the secondary portion thereof, is the critical organ of the genus. Cytologically this has been shown to be the place of karyogamy followed by contraction to the resting condition. Phylogenetically it offers two lines of interpretation: either reduced or increasing development. Both ideas are extant in the literature as applied to relationships within the Auriculariaceae, and between them and other groups.

In the Auriculariaceae, Neuhoff constructs a phylogenetic scheme involving both tendencies. He considers the genus *Iola* the crucial one, for there the basidium arises from a terminal cell and is divided into hypobasidium and epibasidium, the former remaining distinct. This gives rise to two main lines, one showing reduction in differentiation of the hypobasidium, the other increasing emphasis. The first of these is subdivided into a series in which reduction eventually leads to complete suppression, as illustrated by the genus *Helicobasidium*; and another in which the hypobasidium is present though it may be reduced to a vestigial condition, as read in the series

*Achroomyces*, *Tjibodasia*, and *Auricularia*. The second line emphasizes the hypobasidium through the thickening of its walls and the introduction thereby of a resting period. This plan of development is illustrated by the genera *Cystobasidium* and *Septobasidium*. In the latter there are especially critical characters, for the thickening of the walls in some species is so advanced that in view of that and a consequent resting period, the hypobasidium is known as a sclerobasidium. This condition then is strongly like that of the rust teliospore. Indeed, the only real basidial difference between this and such primitive rusts as *Gallowaya* is the catenulate nature of the teliospores of the latter. Consequently, Neuhoﬀ sees here a direct link to the Uredinales through such a genus, for instance, as *Uromyces*, whose teliospores are borne singly on the hyphae. Hence the sclerobasidium (encysted hypobasidium) and the teliospore are homologous.

That there is a close relationship between the Auriculariaceae and the Uredinales is argued by more than mere analogy. Cytologically it is demonstrable that the teliospore and hypobasidium are strictly homologous; likewise the promycelium and epibasidium; sporidia and basidiospores. Möller was the first to comment on this, but to him the hypobasidium of *Helicogloea* and the teliospore were homologous because both were the assembling point of materials necessary for basidium production. Since in the former no resting period was involved there was no need for a heavy wall. This ecological interpretation has since been replaced by the more substantial cytological one. Moreover, the ecological argument lost credibility as investigations revealed that the teliospore is not necessarily designed for wintering over, for there are rusts whose teliospores germinate at once. Again there are rusts whose teliospores are thin-walled, just as in *Septobasidium* of the Auriculariaceae, where the development passes from species with thin-walled, non-resting hypobasidia—hardly more than a stage in development—to thick-walled, persistent forms which rest (winter-over) before germinating. Such striking parallelisms emphasize the closeness of the auriculariaceous fungi and the rusts.

The majority of writers have adhered to de Bary's ('84) tenets that the Uredinales constitute the most primitive of the basidiomycetes. Recently Linder ('29) and Pady ('33) have stressed this by deriving the auriculariaceous forms from the Uredinales. Thus Linder, starting with the Uredinales would, by reduction of the hypobasidium, lead the developmental line through *Septobasidium* and *Cystobasidium* to *Iola* with secondary branches to *Helicogloea* and *Auricularia*. *Septobasidium* holds the closest connection with rusts, since it is parasitic. It stands as a source of further development by reason of two different hypobasidial expressions: thick-walled forms which are adapted for wintering-over and thin-walled forms which have no resting period prior to germination and which really are no more than a stage in development. The latter affords a link to *Iola*, a parasitic form whose thin-walled hypobasidia likewise germinate at once. *Helicogloea* has lost both the parasitic habit and the thickened hypobasidia. *Auricularia* is even more reduced, for there the hypobasidium is represented only as a stage. Specifically, by virtue of the clavate type of hypobasidium, Linder regarded *Helicogloea intermedia* as the form transitional between the rusts and *Iola*. To achieve such a step from rusts to auriculariaceous species, there must be postulated the concomitant factors—reduction of aeciospores to binucleate conidia, development of an extensive fruiting body, and finally a change from parasitic to saprobic habit.

In opposition to such a derivative scheme it may be contended that it is more logical to derive aeciospores from binucleate conidia. This Neuhoff has expressed when he homologized the aeciospores with diploid conidia known in the Auriculariaceae and the pycniospores with haploid conidia. Thus the variety of secondary spore forms in the rusts cannot be said to constitute an obstacle to relationships between the two groups in light of the occurrence of both haploid and diploid conidia in the Tremellales. Especially does the argument of transition from parasitic to saprobic habit seem untenable. As Janchen ('23) has remarked, an attempt at

phylogenetic elucidation must be not only morphologically acceptable, but ecologically comprehensible as well, if it is to be satisfactory. And exactly in its ecological expression does this derivation of Auriculariaceae from Uredinales seem to fail. The high specialization attained by the rusts much more clearly marks them as an end term of a series than as a derivation point. The reverse derivation—the rusts from auriculariaceous forms—is not inconceivable ecologically when one considers the numerous examples of parasitic species of Auriculariaceae.

The foregoing discussion is intended only to summarize some of the more outstanding phylogenetic interpretations in the literature. In view of the greater defensibility of the derivation of the rusts from the Auriculariaceae, that plan is upheld. *Helicogloea* is regarded therefore as representing a simple auriculariaceous type showing tendencies which could lead to the development of an independent hypobasidium and hence to a true teliospore.

#### SUMMARY

1. *Helicogloea* Pat. takes precedence over *Saccoblastia* Möll. with corresponding transfer of recognized species. *Saccoblastia ovispora* and *S. sebacea* are both regarded as synonyms of *Helicogloea Lagerheimi* Pat.

2. In *Helicogloea Lagerheimi* Pat. the basidial primordium is a two-nucleate hyphal cell, producing a lateral expansion.

3. The dikaryon migrates into the expanded portion of the hypobasidium where fusion takes place.

4. Following contraction to the resting condition the secondary nucleus migrates through the primordial portion into the elongating epibasidium, which has arisen apically from the primordium.

5. The two meiotic divisions always take place in the enlarged portion of the epibasidium. The latter segments into four cells and each segment produces a sterigma and a spore or an accessory appendage bearing a sterigma and a spore.

6. Spore germination is by repetition.

7. Morphological development is various in relation to the nuclear cycle; it has been found to correspond to one of three patterns, designated as I, II, and III.

8. The basidium complex is composed of hypobasidium and epibasidium, *sensu* Neuhoff. The former comprises two morphologically distinct parts: the primordium, or primary portion, and its lateral expansion, the "sac," or secondary portion.

9. Within the genus there is seen a progressive sequence from simpler to more advanced forms of basidia, the clavate hypobasidium of *H. intermedia* being interpreted as the most primitive.

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## EXPLANATION OF PLATE

## PLATE 7

*Helicogloea Lagerheimi*

All figures have been drawn with the aid of an Abbé camera lucida. Magnifications are given for each figure.

Figs. 1-13 inclusive show the morphological development of the basidium from the primordial stage through the mature basidium with spores. The nuclear conditions are representative only for these particular examples. All figures  $\times 1100$ .

Fig. 1. Enlarged terminal hyphal cell, the basidial primordium, with two nuclei.

Fig. 2. Production of the hypobasidium as a lateral expansion of the primordium.

Fig. 3. Hypobasidium enlarging, the nuclei moving toward the enlarging secondary portion of the hypobasidium.

Fig. 4. Mature hypobasidium with two nuclei in it.

Fig. 5. Mature hypobasidium with fusion nucleus; epibasidium arising at the apical end of the primordium.

Fig. 6. Nucleus migrating through the primordium; hypobasidium collapsing as the protoplasm withdraws; epibasidium elongating.

Fig. 7. Continued elongation of the epibasidium and withdrawal of protoplasm from the hypobasidium.

Fig. 8. Nucleus in enlarging epibasidium; hypobasidium entirely empty.

Fig. 9. Enlarging epibasidium.

Fig. 10. Epibasidium bending over.

Fig. 11. Epibasidium two-septate, following the first meiotic division; protoplasm withdrawn partly from lower portions.

Fig. 12. Epibasidium three-septate, 4-nucleate; budding sterigmata; the lower portions of the epibasidium collapsing, completely drained of protoplasm.

Fig. 13. Mature basidium with spores in place.

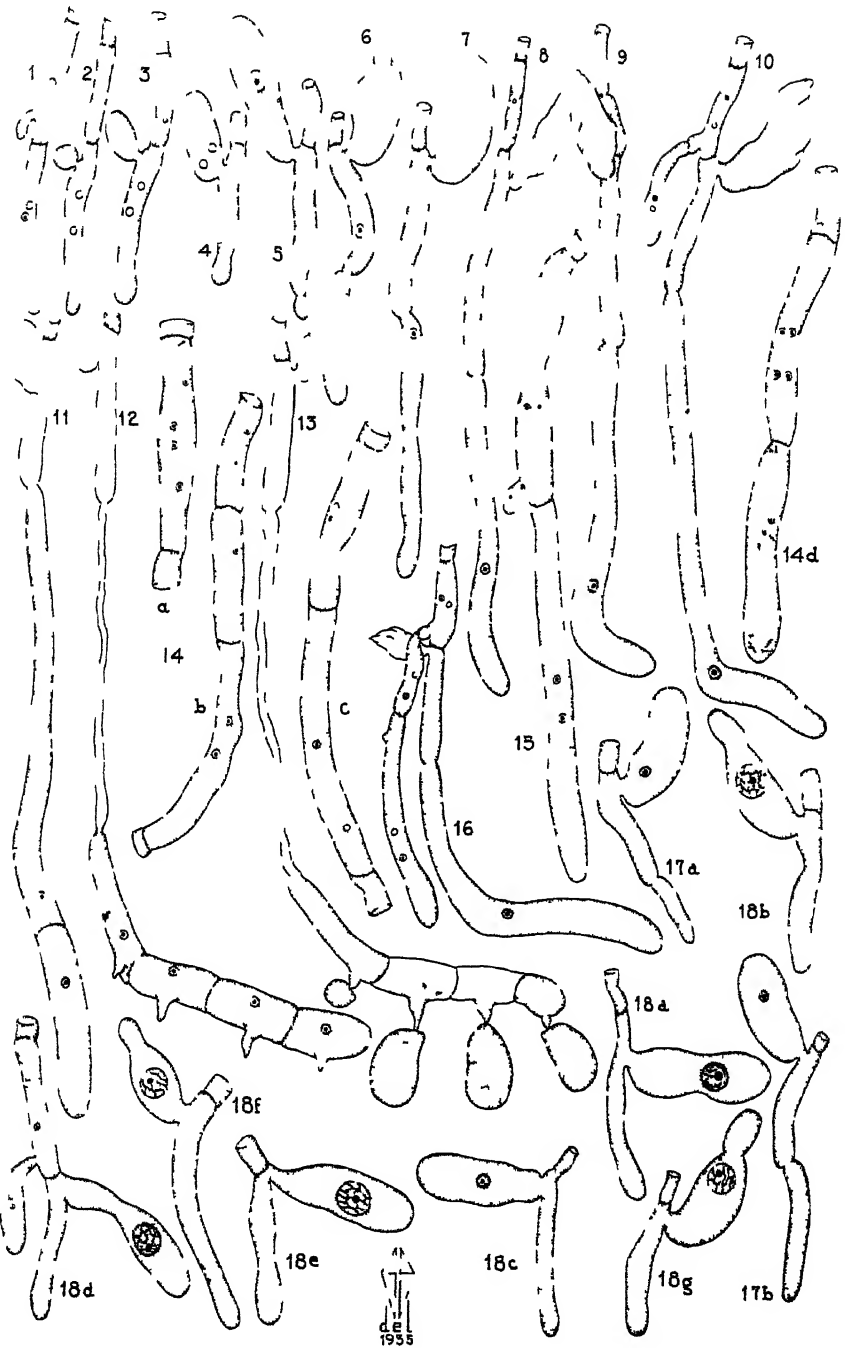
Fig. 14. Hyphal cells. a, d, young cells in which four nuclei are present, for the wall is not yet formed; b, c, older cells with increased reduction of protoplasm.  $\times 1865$ .

Fig. 15. Origin of a branch from a subterminal cell; the terminal cell constitutes a basidial primordium.  $\times 1865$ .

Fig. 16. Basidial proliferation. (See also fig. 18d.)  $\times 1100$ .

Fig. 17. Developing epibasidia showing a crimp between the epibasidium and hypobasidium.  $\times 1100$ .

Fig. 18. Variations in hypobasidial form. a, b, constricted hypobasidia; c, horizontal hypobasidium; d, e, pendent hypobasidia; f, g, extreme distal constriction.  $\times 1100$ .



## EXPLANATION OF PLATE

## PLATE 8

*Helicogloea Lagerheimi*

Fig. 19. Composite view of the fructification on a wood substratum as seen in section.  $\times 464$ .

Fig. 20. Scales to illustrate the proportion of fruiting and hyphal regions in differently developed fructifications.  $\times 100$ .

Fig. 21. a, b, basidia arising from lateral branches.  $\times 1100$ .

Fig. 22. Origin of epibasidium prior to appearance of hypobasidium.  $\times 1865$ .

Fig. 23. a, b, c, irregular, lateral production of epibasidia. Surface level of the fructification marked.  $\times 1100$ .

Fig. 24. Type I of nuclear migration from the hypobasidium.  $\times 1100$ .

Fig. 25. Type II of nuclear migration from the hypobasidium. a, typical form; b, unconstricted type.

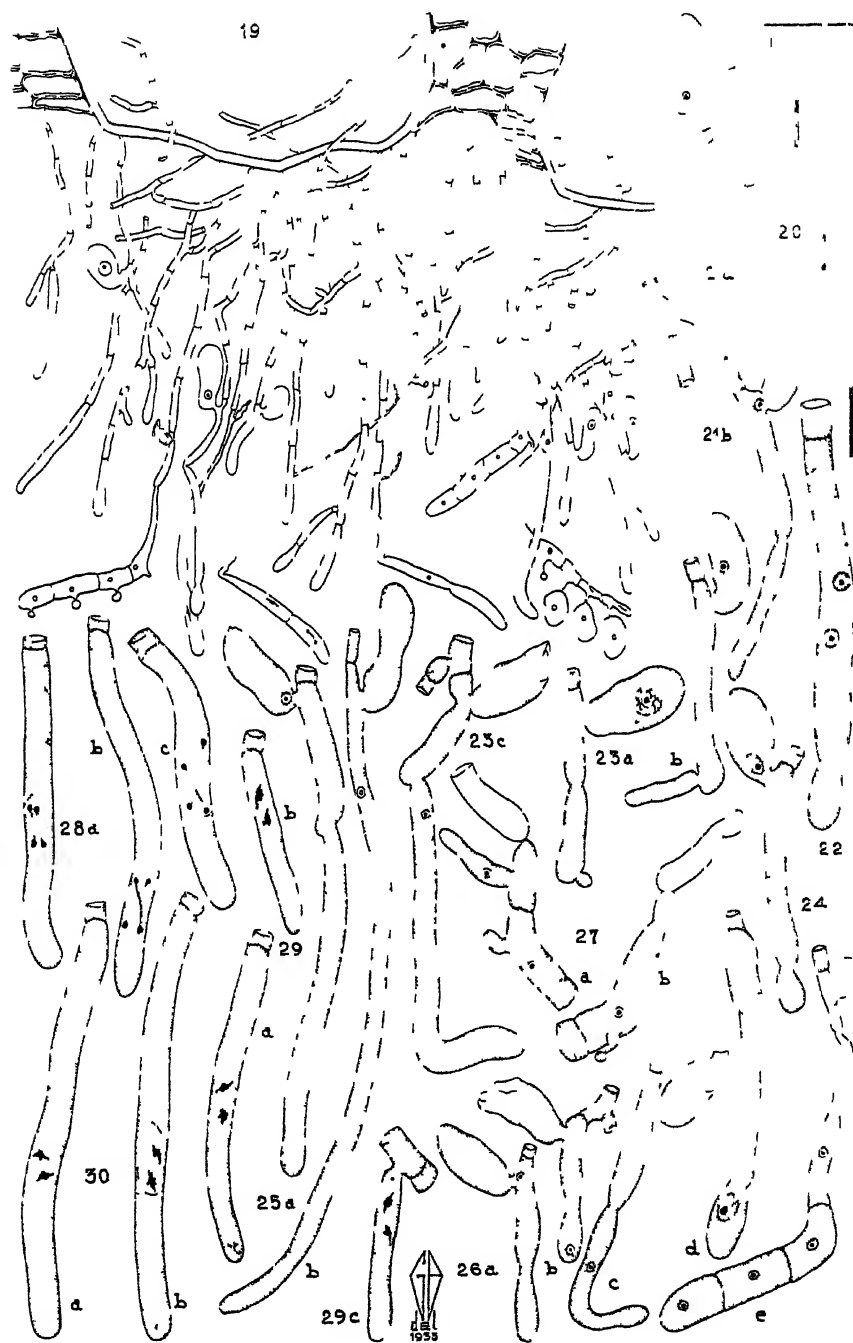
Fig. 26. a, Type III of nuclear migration. b, c, d, e, subsequent development.

Fig. 27. a, deep constriction and septum at the base of the fourth segment of the epibasidium; b, constriction without a wall.  $\times 1100$ .

Fig. 28. a, conjugate mitosis, with nearly parallel orientation; b, c, crossed spindles.  $\times 1865$ .

Fig. 29. a, b, c, mitotic division figures indicating future crossed orientation of the spindles. In c a remnant of the nucleolus is visible.  $\times 1865$ .

Fig. 30. Mitosis. a, membranes completely broken down, nucleoli still visible; b, nuclear membranes present in part, nucleoli distinct.  $\times 1865$ .



## EXPLANATION OF PLATE

## PLATE 9

*Helicogloea Lagerheimi*

Fig. 31. a, basidial primordium with the basal wall just formed; b, older primordium with hypobasidium and epibasidium both developing.  $\times 1865$ .

Fig. 32. A series to show the increase in size from the initiation of the primordium through the hypobasidium production.  $\times 1865$ .

Fig. 33. Origin of the hypobasidium. (See also fig. 31b.)  $\times 1865$ .

Fig. 34. a, b, nuclei in close association previous to migration into the hypobasidium.  $\times 1865$ .

Fig. 35. Lag of second nucleus in passage into hypobasidium.  $\times 1865$ .

Fig. 36. a, b, nuclei moving into hypobasidium. In b the first nucleus is prematurely enlarged prior to fusion.  $\times 1865$ .

Fig. 37. Nuclei in hypobasidium previous to fusion. Note effect of streaming protoplasm.  $\times 1865$ .

Fig. 38. Nuclear fusion. a, nuclei touching, nuclear membranes still intact; b, nuclei as in a, but enlarged and showing a reticulate nature; c, nuclear membranes broken down and the contents mingling; d, nuclei fusing, one larger than the other with slightly more pronounced reticulations; e, nuclei of different sizes corresponding to their development, both deeper in the hypobasidium than usual.  $\times 1865$ .

Fig. 39. Fused nuclei with an indentation between the two still apparent. Within the common membrane there is an advancing net development.  $\times 1865$ .

Fig. 40. a, b, c, stages in nucleolar fusion.  $\times 1865$ .

Fig. 41. a, post-fusion nucleus, with strongly developed network; b, post-fusion nucleus with prominent chromatic beads scattered on the threads.  $\times 1865$ .

Fig. 42. a, nucleus contracting, the network still pronounced; b, nucleus in resting condition, completely contracted.  $\times 1865$ .

Fig. 43. a, b, c, examples of nuclear passage from hypobasidium; a, detail of fig. 24; c, detail of fig. 25.  $\times 1865$ .

Fig. 44. Variation in the initiation of prophase activity. a, nucleus enlarged, reticulate.  $\times 1865$ . b, nucleus still in primordial portion.  $\times 1100$  with detail  $\times 1865$ .

Fig. 45. Prophase in sporogenous part of the epibasidium. a, nuclear membrane intact, nucleolus peripheral, network appearing opposite pole of nucleolus; b, the network appearing slightly polarized; c, faint reticulations in enlarged nucleus from epibasidium of Type III. All  $\times 1865$ .



## EXPLANATION OF PLATE

## PLATE 10

*Helicogloea Lagerheimi*

Fig. 46. Prophase of first meiotic division. The nucleus is elongate, conforming to the shape of the epibasidium.  $\times 1100$  with detail  $\times 1865$ .

Fig. 47. Early prophase with chromatic beads on the threads.  $\times 1865$ .

Fig. 48. Prophase. a, nucleolus, slightly diminished in size, lying at anterior pole and the threads grouped at the opposite pole.  $\times 1865$ ; b, nucleolus still prominent, the threads less massed and central in position.  $\times 1100$  with detail  $\times 1865$ ; c, later prophase, the nucleolus at the periphery, the chromatin densely massed.  $\times 1865$ .

Fig. 49. Early prophase from an epibasidium with a development corresponding to Type III.  $\times 1865$ .

Fig. 50. Anaphase. a, intranuclear spindle with scattered chromosomes. Remnants of the nucleolus are visible within the membrane and centrosomes are present at the poles. b, nuclear membrane present in part; nucleolus sharp; c, d, e, membranes broken down and spindles free in cytoplasm; the nuclei have disappeared.  $\times 1865$ .

Fig. 51. Late anaphase. a, nuclear membrane discernible in part, the nucleolus distinct in the cytoplasm; b, membrane entirely gone, chromosomes massing together as they move to the poles; c, spindle contracted, chromosomes clumped, massing at the poles. The clearer areas at the poles denote the position of the daughter nuclei.  $\times 1865$ .

Fig. 52. Telophase. c, chromosomes massed at the poles, the two groups still connected by distinct fibers, daughter nuclei organizing; b, daughter nuclei more prominent and the fiber connections diminishing; c, lower nucleus nearly completely organized, the upper not so advanced; fibers prominent in upper region where they are still attached to the nucleus; d, darker area on connecting fibers indicative of wall formation.  $\times 1865$ .

Fig. 53. Two-nucleate stage. a, upper nucleus completely organized, lower nucleus still showing fiber connections; the wall is just coming in; b, wall just formed and the nuclei farther apart than in a.  $\times 1865$ .

Fig. 54. Two-nucleate stage. The nuclei are reorganized but the wall is not yet formed. A clearer zone shows its future position.  $\times 1865$ .

Fig. 55. Second meiotic division. Both spindles are in anaphase, the nuclear membranes have disappeared as well as the nucleoli.  $\times 1865$ .

Fig. 56. Variation in the synchronization of the second meiotic division. a, lower nucleus in anaphase, nucleolus distinct; upper nucleus in telophase.  $\times 1865$ ; b, lower nucleus in telophase with fiber connections still visible and the wall coming in; upper nucleus nearly completely organized, the fibers still just discernible.  $\times 1865$ ; c, daughter nuclei of lower segments completely formed with a wall between; basal nuclei still in telophase with connecting fibers between.  $\times 1100$  with detail  $\times 1865$ .





## EXPLANATION OF PLATE

## PLATE 11

*Helicogloea Lagerhermi*

Fig. 57. Four-nucleate, four-septate epibasidium, two of the walls having just been formed.  $\times 1865$ .

Fig. 58. a, fourth segment of epibasidium with a basal septum; b, fourth segment with protoplasmic remnants simulating a septum.  $\times 1865$ .

Fig. 59. Segment from an epibasidium with a nucleus showing two nucleoli.  $\times 1865$ .

Fig. 60. Budding sterigmata. The wall is not completely formed between the two end cells.  $\times 1865$ .

Fig. 61. Sterigma with spore developing on the second segment of the epibasidium.  $\times 1865$ .

Fig. 62. Sterigmatic formation. In segments 2 and 3 the nuclei are changing form preparatory to passing into the spores.  $\times 1865$ .

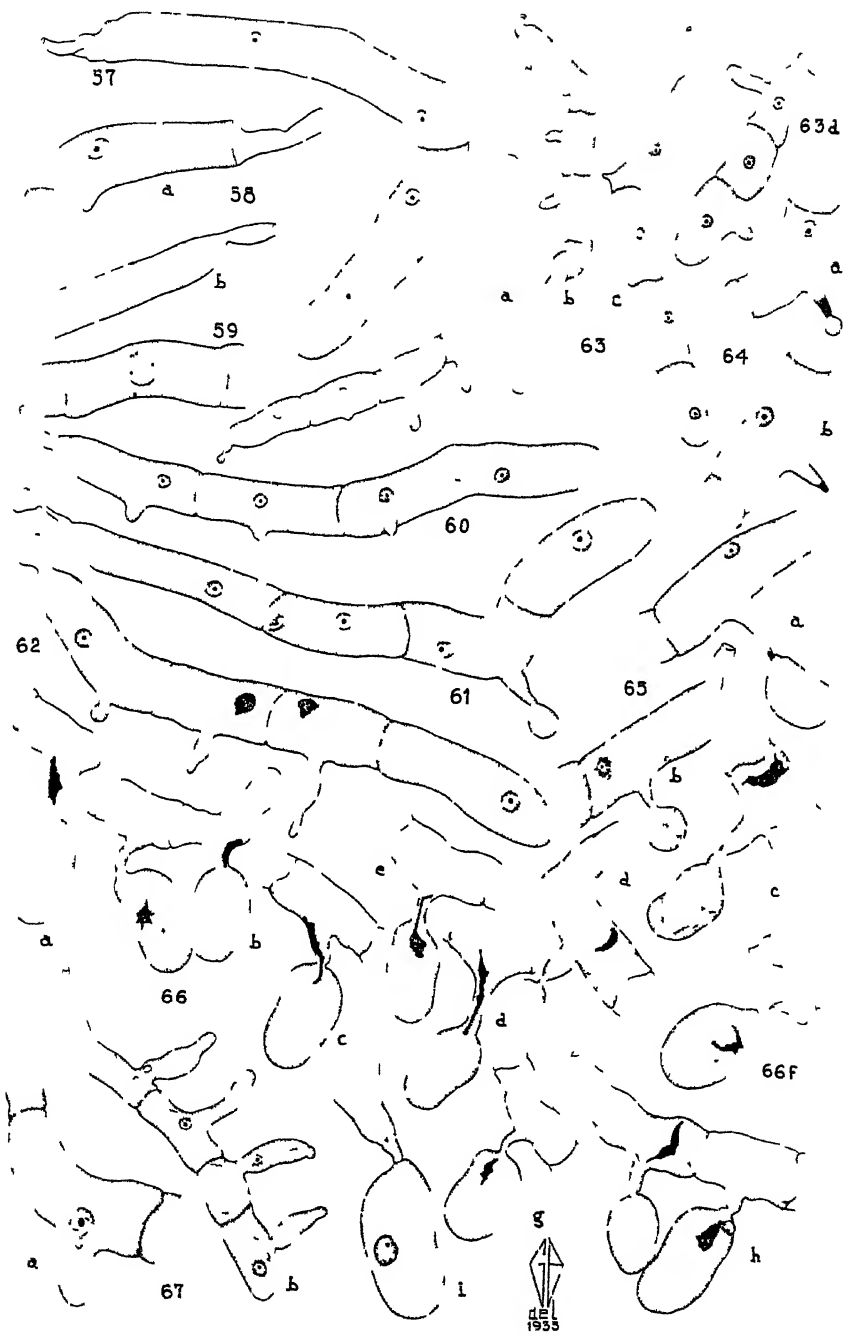
Fig. 63. Variations in sporogenous portion of the epibasidium. a, apical segment with typical sterigma; lower segments developing longer appendages; surface level marked; b, apical segment producing long appendage; surface level marked. Note the bend in the basal segment. c, sterigmatic initiation in the fourth segment; d, sterigmata forming on opposite sides. All  $\times 1100$ .

Fig. 64. a, b, developing sterigmata with dark staining tips.  $\times 1865$ .

Fig. 65. Nuclear behavior preparatory to passage into the spores. a, nucleus normal, spore about half developed. Note that the dark-staining tip is still apparent; b, nucleus becoming deeply stainable; protoplasm withdrawing into the developing spore; c, nucleus dark-staining, irregular, attenuate; d, nucleus a homogeneous dark mass. All  $\times 1865$ .

Fig. 66. Nuclear passage into the spore. a, nucleus in sterigma; b, nucleus of end segment, in sterigma; second segment completely drained of protoplasm and nucleus reorganizing in the spore; c, d, nuclei much drawn out in passage through the sterigmata; e, nucleus mostly within the spore; f, g, nuclei not yet reorganized in the spores; h, one nucleus reorganizing in the spore, nucleus of the basal segment ready to migrate; i, nucleus reorganized in the spore. All  $\times 1865$ .

Fig. 67. a, nucleus moving into a long appendage without change in form.  $\times 1865$ ; b, sporogenous portion of an epibasidium, all segments of which have produced long appendages.  $\times 1100$ .



## EXPLANATION OF PLATE

## PLATE 12

*Helicogloea Lagerheimi*

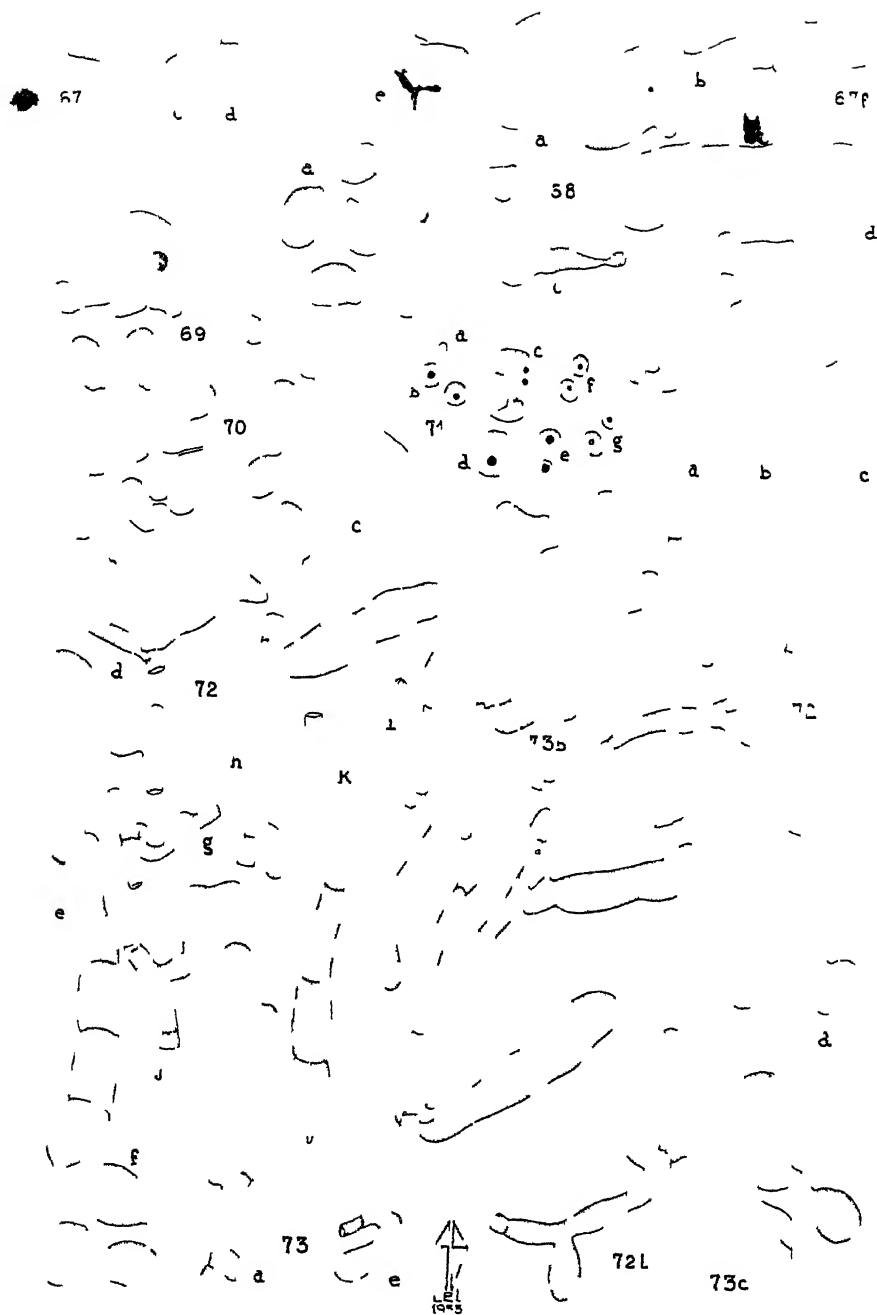
Fig 67 c, d, formation of sterigmata and spores at the ends of long appendages. Nucleus unchanged at this stage. Surface level marked in d, e, f, nuclei prematurely changed for passage into sterigmata and spores. All  $\times 1865$

Fig 68 a, typical spore b, spore germinating while still attached to the sterigma, c, d, germination by repetition  $\times 1865$

Fig 69 Nucleus changing for passage through germ tube and sterigma into secondary spore  $\times 1865$

Fig 70 Germination of spores in hanging drop cultures a, stages prior to germ tube production, 24 hours, b, production of germ tubes and secondary spores, 24-48 hours, c, protoplasm withdrawn into secondary spores, 72 hours. All  $\times 734$

Fig 71 Nuclei showing varying sizes through the cycle and corresponding nucleolar volumes. All from the same section and  $\times 1865$  a, dikaryon from terminal hyphal cell, b, dikaryon prior to migration into hypobasidium, c, fusion nucleus in hypobasidium d, post fusion, nucleus contracting, nucleolar volume obviously increased, e, nuclei from migrating stages after fusion, f, nuclei from 4 celled stage of epibasidium prior to sterigmatic formation, g, nuclei from typical spores



## EXPLANATION OF PLATE

## PLATE 13

Fig. 72. *Helicogloea pinicola*, No. 20124. a, forked hypobasidium; b, budding epibasidium sub-apical in position; c, budding epibasidium slightly sub-apical in position; d, typical hypobasidia; e, septate epibasidium; f, spores; g, clamp connections on the hyphae.

No. 20555. h, slightly constricted hypobasidium; i, j, forked hypobasidia; k, septate epibasidium with a fourth septum present; l, sub-apical epibasidium. All figures  $\times 434$ .

Fig. 73. *H. pinicola* f. *alnovidis*. a, origin of epibasidium, hypobasidium forked; b, irregular hypobasidium, typical epibasidium; c, septate epibasidium, two segments of which are already discharged; d, germinating spore; e, proliferation of basidia. All  $\times 434$ .

Fig. 74. *Helicogloea graminicola*. a, origin of the hypobasidium; b, mature hypobasidium; c, septate epibasidium. Note that all the protoplasm has not withdrawn from the hypobasidium. d, spores. All  $\times 434$ .

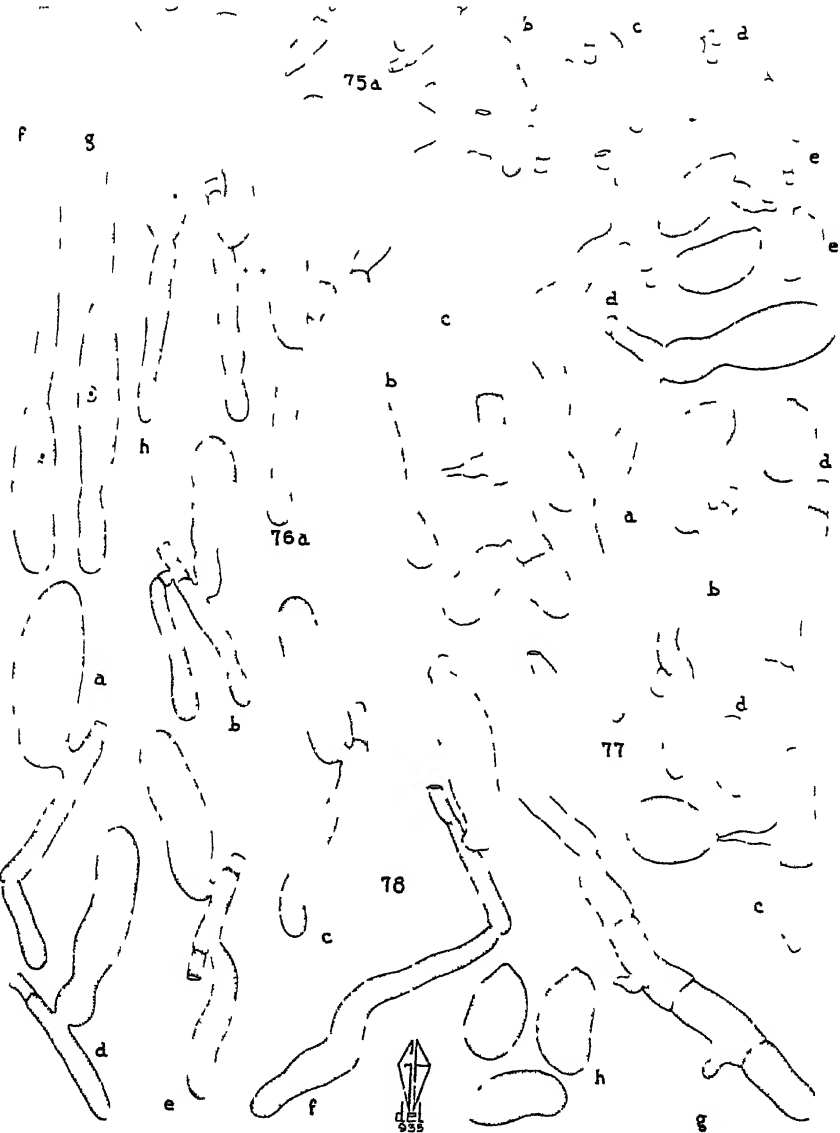
Fig. 75. *Helicogloea intermedia*. a, constricted hypobasidium; b, origin of the epibasidium, hypobasidium much constricted; c, basal constriction of hypobasidium; d, typical origin of epibasidium; e, proximal production of epibasidium or basal constriction; f, g, h, stages in the development of the clavate type of hypobasidium. All  $\times 734$ .

Fig. 76. *Helicogloea caroliniana*. a, variation in the hypobasidium; b, epibasidium; c, epibasidium with developing sterigmata and spore; d, long appendage with sterigma and spore; e, mature spores. All  $\times 1100$ .

Fig. 77. *Helicogloea Lagerheimi*, No. 42262, marked as var. *vulgaris*. a, constricted hypobasidium, typical epibasidium of terminal origin; b, intercalary origin of the basidium; c, septate epibasidium with four septa; two segments have already discharged their spores; d, spores. All  $\times 1100$ .

Fig. 78. *Helicogloea Lagerheimi*, Rick's material. a, typical hypobasidium and epibasidium; b, c, d, variously constricted hypobasidia; e, intercalary origin of basidium; f, developing sporogenous portion of epibasidium; g, epibasidium developing sterigmata; h, spores. All  $\times 1100$ .

74a



## EXPLANATION OF PLATE

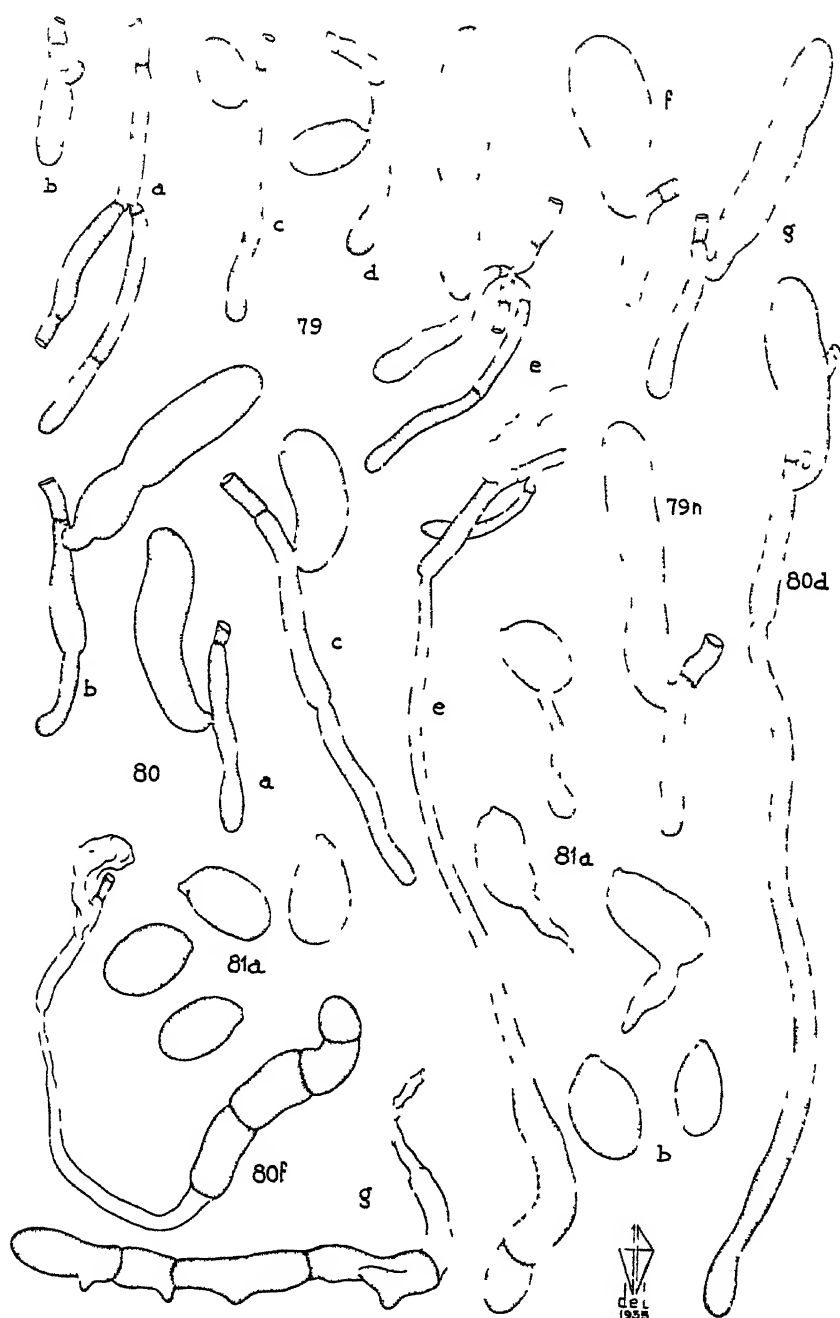
## PLATE 14

*Helicogloea Lagerheimi*, type material

Fig. 79. a, terminal primordium and hyphae; b, slightly older primordium with origin of hypobasidium; c, hypobasidium more advanced; d, hypobasidium unusually far forward on primordium; e, large, constricted hypobasidium; f, short broad hypobasidium; g, long slender hypobasidium; h, unusually long hypobasidium. All  $\times 1100$ .

Fig. 80. a, epibasidium just distinguishable; b, epibasidium slightly more advanced; c, epibasidium elongating, hypobasidium emptying; d, epibasidium prior to thickening of sporogenous portion; e, sporogenous portion two-celled; f, sporogenous portion four-celled; g, sporogenous portion four-septate with sterigmata. All  $\times 1100$ .

Fig. 81. a, four spores; b, three germinating spores; c, one large, one small spore. All  $\times 1100$ .







# MORPHOLOGY, PHYSIOLOGY AND CYTOLOGY OF SYRINGOSPORA INEXORABILIS (MONILIA INEXORABILIS)

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While we were studying pathogenic species of *Zymonema*, Mazza and Palamedi ('32) described *Monilia inexorabilis* from a fatal case of blastomycosis of the skin and mucosa. His illustrations showed an imperfect stage which closely resembled some seen in lesions and in cultures of species of *Zymonema*. Dr. Mazza kindly sent us a culture, and although the organism has been grown for four years on a great variety of media, it has not shown any trace of sexuality or ascospore formation such as is common in *Z. dermatitidis* and *Z. capsulatum*. The study was resumed early in 1934, and sufficient morphological and cytological data have now accumulated to warrant their presentation.

The patient was a Spaniard, 53 years of age, who had lived for 21 years in the Chaco of Argentina. Ulcerating lesions on the buccal mucosae were diagnosed as blastomycotic, and a biopsy confirmed the diagnosis. The lesions were of a progressive nature and involved the whole respiratory tract, becoming generalized. A complete autopsy established this as "true" blastomycosis.

We gratefully acknowledge Dr. Salvador Mazza, Jefe de la Misión de Estudios de Patología Regional Argentina, for cultures of this organism, and the Science Research Fund of Washington University for a grant in aid of this work.

Issued March 20, 1936.

## METHODS OF TECHNIQUE

For a morphological study of the organism, mounts of mycelium were made in Amann's lacto-phenol and 0.5 per cent cotton blue. Distilled-water mounts were also favorable because their uniform staining did not distort the material. Several dyes, such as 1 per cent aqueous crystal violet to the desired intensity in glycerine, methylene blue, neutral red, and iodine green, were used to bring out granulation. The life cycle of the fungus was observed from hanging-drop preparations made with lactose broth, nutrient broth (meat extract), and 2 per cent proteose peptone. Iodine potassium iodide (saturated solution) was used for studying the glycogen content of the cells and the possible chondriosomes, as advocated by Guilliermond; neutral-red and methylene blue, for studying volutin or metachromatic material. A pinch of benzidine sulphate added to a water mount of organisms showed the so-called "dancing bodies." Osmic acid 2 per cent, and platinic chloride 5 per cent, demonstrated fat and lipoidal substances.

For a study of the nuclear phenomena, agar slants of the culture were killed and fixed with Hermann's fluid and embedded in celloidin (Moore, '33). Sections were then cut to a thickness of 10  $\mu$ , and stained with Haidenhain's iron-alum haematoxylin with no counterstain. After being cleared in benzol they were mounted in Canada balsam. When embedded in celloidin the material has little or no shrinkage and is cleared very nicely.

## DESCRIPTION

The organism was obtained on a Sabouraud's glucose agar slant. In the host the parasite exists as a single or budding yeast-like cell which may very easily be confused with that found in blastomycosis. When cultivated on an artificial substrate, the cells send out germ-tubes or elongate (pl. 15, figs. 1-4) to produce hyphae of cells which are formed by the development of cross-walls (figs. 5-6). These vary from 2 to 5  $\mu$  in diameter according to the medium on which grown. On several media, however, the yeast-like budding cells may per-

sist, or at least predominate for a variable length of time (figs. 9, 25), and measure from 2 to 17  $\mu$  in diameter. Wort agar is especially adapted for the continuance of the yeast stage, and blood agar and serum media, to a certain degree (figs. 24-25).

The continued growth as a saprophyte results in morphological changes which help in the classification of these yeast-like fungi. The elongated forms developing from the germinating cell vary both in diameter and length. On media with beef extract near the neutral point or with a high pH, the filaments generally are long and have a small diameter (figs. 10-11, 23). On media with a low pH, as Raulin's malt extract, Czapek's, or wort agar, the cells are shorter and have a greater diameter (figs. 8-9, 12-13, 16-17). On wort agar (fig. 12) the organism becomes very large, spherical, and thick-walled. This peculiar condition is noticed to a lesser degree on malt extract agar (fig. 9), which is a modification of wort agar.

A verticillate or dendroid type of growth is rather common on most media for this fungus, but definitely characteristic on Raulin's solution (figs. 16-17). The cells of the main axes of the structure (fig. 17) are somewhat longer than those which bud off from them, the blastospores. The blastospores develop along with the hyphae as single or multiple cells, terminally (figs. 16-17, 20, 22), laterally (figs. 8, 10, 18-23), or at the point of division of two elongated cells of the filaments (fig. 17). They may either be spherical to ovoid or subpyriform to pyriform, and measure approximately 3-6  $\mu$  in diameter, usually 5  $\mu$  or more. These cells are uninucleate and are capable of developing new colonies if allowed to germinate under favorable conditions.

Besides the structures mentioned, there are also large terminal, clavate or obovate cells measuring 9-15  $\mu$  in diameter or long axis. They are double-contoured (thick-walled) structures and are found as modified cells on malt extract, glycerine, yeast dextrose, nutrient blood agar, and even in serum. Lanceolate cells 9-15  $\mu$  in long axis also occur, usually singly or budding, and are modifications of the spherical or ovoid cells found on various substrates. Another structure noted is the

thick-walled cell or cells sometimes found at the base of a verticillate growth (fig. 16). These are the germ cells which develop a thickened wall in much the same manner as would the root of a plant.

The nuclear phenomena of development will be considered under cytology.

### CULTURAL CHARACTERISTICS

The organism when received was growing on a Sabouraud's agar slant. Subcultures from this growth were made on a number of different media, varying in hydrogen ion concentration, protein or protein decomposition products as peptones, and in the amounts of carbohydrate and nitrogen. All cultures were grown at room temperature, approximately 22° C., on the following media arranged in the order of increasing pH.

*Rawlin's solution (pH 4.1).*—Sediment of growth on bottom of flask. Culture monilioid. Groups of budding yeast-like cells, double contoured, 5–12  $\mu$  in diameter. Filaments 2–5  $\mu$  in diameter; blastospores 3–5  $\mu$  in diameter; mycelium verticillate.

*Czapek's Agar (pH 4.4).*—Colony approximately 3.5 cm. in diameter after 40 days. Mycelium mostly submerged in agar, tending to form coremia of elongated cells approximately 3  $\mu$  in diameter. Spherical and ovoid, yeast-like cells 3–17  $\mu$  in diameter; racquet and verticillate mycelium; blastospores of varying proportions, spherical to ovoid.

*Malt Extract Agar (Difco, pH 4.6).*—Colony approximately 3.5 cm. in diameter after 40 days. Mycelium submerged in medium, with a general appearance similar to that on Czapek's agar. Color creamy-buff. Hyphae approximately 3  $\mu$  in diameter; blastospores approximately 6  $\mu$  in diameter. Budding cells 6–12  $\mu$  in diameter on surface of medium, with branching, coremioid mycelium. Terminal clavate, obovate to lanceolate cells approximately 12–15  $\mu$  in long axis.

*Wort Agar (Difco, pH 4.8).*—Colony approximately 3.5 cm. in diameter after 40 days. Color light coffee-brown. Culture

shows excrescences. Verticillate growth of cells 3–15  $\mu$  in diameter, the large spherical cells having a thick capsule. Budding cells present. Filamentous mycelium approximately 3  $\mu$  in diameter, in medium, with some elongated cells and blastospores approximately 4  $\mu$  in diameter. Terminal obovate to lanceolate cells present.

*Sabouraud's Agar (pH 5.6).*—Colony approximately 5 cm. in diameter after 40 days. Most of culture submerged, portion on surface approximately 2.5 cm. in diameter with a heaped-up growth in center. Growth excrescences and radiating ridges to the exposed periphery evident. Color dark creamy-buff. Submerged mycelium filamentous, 2–5  $\mu$  in diameter, branching, coremioid and somewhat verticillate. Blastospores approximately 6  $\mu$  in diameter. Yeast-like, budding, also germinating, cells 3–12  $\mu$  in diameter. Obovate or clavate terminal cells on submerged filaments. Surface growth of yeast-like cells.

*Corn-Meal Agar (Difco, pH 6.0).*—Colony approximately 3.5 cm. in diameter after 40 days. Culture almost entirely submerged with a surface growth approximately 0.7 cm. in diameter. Color dull creamy-buff. Macroscopic appearance similar to that on Czapek's agar. Surface growth of yeast-like budding cells, same as on Sabouraud's agar. Filaments much thickened, branching, coremioid; blastospores thick-walled, approximately 5  $\mu$  in diameter.

*Potato-Dextrose Agar (pH 6.2).*—Colony approximately 3.5 cm. in diameter, with an irregular periphery. Growth on surface of yeast-like, budding cells approximately 2–10  $\mu$  in diameter. Submerged mycelium of filamentous forms with hyphae approximately 3  $\mu$  in diameter; blastospores approximately 6  $\mu$  in diameter. Mycelium verticillate as in other substrates.

*Potato-Dextrose Broth (pH 6.2).*—Sediment at bottom of flask. Mycelium similar to that on the agar.

*Nutrient Agar (Difco, pH 6.6).*—Colony moist and irregular with growth partially submerged in agar, approximately 2.5

cm. in diameter. Cells on surface mostly spherical to ovoid, budding, up to  $12\ \mu$  in diameter. Large cells  $15\ \mu$  in diameter. Large spherical cells within medium and smaller ovoid to spherical forms on surface.

*Nutrient Broth (Difco, pH 6.7).*—Sediment at bottom of flask. Yeast-like cells as on the above medium, with filamentous forms monilioid in appearance, approximately  $3\ \mu$  in diameter. Blastospores subpyriform,  $5\ \mu$  in diameter.

*Lactose Agar (Difco, pH 6.8).*—Colony approximately 2 cm. in diameter. Submerged mycelium a verticillate, coremioid growth similar to that in Czapek's agar. Growth on surface moist and cream-colored, with many budding, yeast-like cells, spherical and ovoid,  $3\text{--}12\ \mu$  in diameter. Filaments elongated,  $2\text{--}3\ \mu$  in diameter, monilioid and blasto-dendroid, verticillate; blastospores pyriform, subclavate or ovoid, in varying proportions.

*Glycerine Agar (nutrient agar plus 6 per cent glycerine, pH 7.0).*—Colony approximately 5 cm. in diameter, both submerged in the agar and on the surface. Growth on surface approximately 3.5 cm. in diameter with an irregular periphery, dull cream in color. Central region of erupted, vesicular-like outgrowths. Yeast-like cells spherical and ovoid, singly or in chains,  $3\text{--}9\ \mu$  in diameter. Elongated, branching filaments  $2\text{--}4\ \mu$  in diameter. Subclavate cells terminally on filaments,  $9\text{--}15\ \mu$  in long axis.

*Yeast-Dextrose Agar (Difco, pH 7.0).*—Macroscopic appearance similar to that on nutrient agar. Yeast-like budding cells  $3\text{--}12\ \mu$  in diameter. Filaments monilioid, approximately  $3\ \mu$  in diameter, branching, terminating in a double-contoured ovoid cell  $12\ \mu$  in long axis; blastospores of varying proportions.

*Nutrient Blood Agar (nutrient agar plus bacto-beef blood, pH 7.2).*—Colony approximately 2 cm. in diameter with an irregular periphery. Yeast-like cells double-contoured, mostly spherical, in general  $9\ \mu$  in diameter. Many smaller cells. Filaments  $2\text{--}4\ \mu$  in diameter, cross-walled and branching.

*Serum (Bacto-beef blood serum, pH 7.3).*—Thick sediment at bottom of flask. Mycelium of filaments approximately  $3\ \mu$  in diameter, terminating in a thick-walled, spherical, ovoid or sub-lanceolate cell  $9\text{--}15\ \mu$  in diameter; blastospores in varying proportions.

*Endo's Agar (Difco, pH 7.5).*—Colony approximately 3 cm. in diameter. Mycelium mostly submerged in agar. Many yeast-like, budding cells  $3\text{--}12\ \mu$  in diameter. Hyphae  $2\text{--}4\ \mu$  in diameter. Blastospores spherical, ovoid or pyriform, approximately  $6\ \mu$  in diameter or long axis.

*Carbohydrate reactions.*—Acid and production of gas with dextrose, maltose, levulose, and d-mannose. Acid and no gas with galactose, lactose, saccharose. No acid or gas with l-arabinose, l-xylose, rhamnose, raffinose, mannitol, amygdalin or dextrin.

*Gelatine.*—Gelatine is liquefied.

*Litmus milk.*—Shows no acid or curdling.

### CYTOLOGY

As far as can be determined by the literature, there has been very little work on the cytology of the imperfect yeasts. Rajat ('06) described briefly a species of *Parendomyces* (?) under the name "champignon du muguet." The nuclear phenomena are often important in classification and in questions of phylogeny. The single yeast-like cell is uninucleate (pl. 15, figs. 27–30). The granular nucleus is seen as a large body with a heavily staining nucleolus from which emanates a net-work along which are granules of volutin deeply stained with haematoxylin. As the cell grows older, it elongates (pl. 16, fig. 31) and the cell wall is constricted. The nuclear division which then occurs at the point of indentation is amitotic, of an advanced type. No chromosomes are seen in the division process; instead, as far as could be determined from fixed material, there is a clumping of the metachromatic material in two groups, within the nucleus and opposite to each other (figs.



31-32, 35-36, 38, 42, 50). At this time, within the nucleus, fine reticulations with small granules extend between the two clumps. Directly after division these reticulations seem to spread out (figs. 33, 37, 50) and retain the type of structure seen in the large nuclei (figs. 27, 49).

When the young yeast-like cell or blastospores are allowed to germinate (pl. 15, figs. 1-4), the nucleus elongates, divides within the cell, and the daughter nucleus grows along with the tube as it grows out. In the formation of the cross-wall the daughter nucleus also elongates and divides amitotically as described above, accompanied by an abscission of the cell. One nucleus is thus carried into the newly formed cell. At a later stage, the mother cell divides in two, with one nucleus in each daughter cell, resulting in a uninucleate cell (pl. 16, figs. 39, 46, 48). In many of the yeast-like cells, the nucleus is at the apical portion growing into the newly forming bud (figs. 41-42). As the bud matures, there is an abscission from the mother cell and the nucleus is divided in the process (fig. 43).

The mycelium is uninucleate, with the extended nucleus centrally placed in the long cells (figs. 47-48). It is of interest that the division of a nucleus does not necessarily imply that a new cell is cut off at the same time. A nucleus may divide within a cell and then migrate into a newly formed bud (figs. 33, 36-37, 48-50). This is particularly true in the formation of the blastospores where the nucleus first divides amitotically and then migrates into the young blastospore which consequently is uninucleate.

The presence of a network and heavily granulated protoplasm is noted in all the cells. Except for the blastospores and the clavate, obovate or lanceolate cells which are modifications of the yeast-like cells, there are no distinctive structures in this organism.

*Cellular contents.*—Reserve materials are found normally in larger amounts in the older portions of the mycelium, as glycogen, lipoids, oil globules, metachromatic granules, or volutin, or as decomposition products, as nucleic acid substances, protein derivatives, or carbohydrates. These ma-

terials have been discussed previously in greater detail (Rajat '06; Moore '33, '35).

*Volutin*.—Volutin or metachromatic material may be very easily demonstrated with methylene blue (fig. 54) or even with iron-alum haematoxylin, as substances within the cell, along the inner wall surface, or along the network, both within the nucleus and in the cytoplasm. With the latter dye they stain deeply, whereas with the former they appear as droplets. A pinch of benzidine sulphate added to a water mount of living organisms (fig. 52) reveals a vacuolar condition within which are a varying number of granules known as "dancing bodies." These granules are precipitated volutin in a state of Brownian movement. They take a blue coloration supposedly, because of the action of benzidine on the peroxidases.

*Glycogen*.—With saturated iodine potassium iodide glycogen can be demonstrated very easily (fig. 55), taking an orange-brown coloration. With neutral red it is not quite so clear but appears as a pink or red vacuole called the glycogen vacuole. Glycogen is more abundant in the older than in the younger cells.

*Vacuoles*.—Vacuoles are easily demonstrated with benzidine sulphate (fig. 52), methylene blue (fig. 54), and with iron-alum haematoxylin. In the last case they appear surrounded by the network. Vacuoles are further brought out with iodine, within which are found the crystalloid droplets comparable to those seen with neutral red. They can also be demonstrated with saturated iodine potassium iodide.

*Chondriosomes*.—Chondriosomes are shown with saturated iodine potassium iodide, as demonstrated by Guilliermond. In this fungus they appear as light yellow, refractile bodies or droplets of varying size, distributed within cytoplasmic substance. There are few in the young cells.

*Fat, lipoidal substances*.—In addition to the substances mentioned, there are also fats, lipoidal substances, other reserve materials, and secretion and even excretion products. What

the nature of these substances may be is not entirely clear, but it is known that fatty acids, glycerides, phospholipides, glycerol and phospho-aminolipides (complex lipides) may be present in varying amounts. Several agents were tried to demonstrate them, each showing some advantage. With 2 per cent osmic acid, they are reduced and take a black coloration (fig. 51). In the young cells or filaments, the blackened portions are more abundant at points where the nuclei would be found. Many of the young, yeast-like cells show only a single small droplet, while older cells show numerous irregular globules throughout. With platinic chloride (5 per cent solution) much the same results are obtained (fig. 53). Iodine potassium iodide as applied for glycogen or chondriosomes shows lipoidal substances, as oil droplets, equally as well. These are very small and appear as refractile, hyaline bodies.

#### SYSTEMATIC POSITION

Since the literature dealing with the nomenclature of the imperfect yeasts is voluminous and has been thoroughly summarized in a recent work by the senior author ('35), it need not be reviewed here. *Syringospora* Quinquaud ('68) was based on *S. Robinii*, a renaming of *Oidium albicans* Robin ('53), which in turn was based on the work of Gruby (1842) on the common organism of thrush (muguet, Soor or sapinho). The morphology figured by Quinquaud is similar to that of our species or to that of *Mycotorula* Langeron & Talice ('32) non Will. In our organism, the verticils show some reduction, being less dense than in *S. albicans* and tending to produce one or two branched chains of blastospores at the septa as in the genus *Mycotoruloides*. The verticils of these chains of blastospores are also reduced, approaching a state shown in *Mycocandida* where the verticils normally contain only two blastospores per septum of the axial filament. The blastospores are generally ellipsoidal, rarely clavate or obovate, never pyriform or lacrimiform as those of *Blastodendrion*. Thick-walled cells (perhaps chlamydospores) appear to be basal either to a whole pseudo-mycelium or to a primary branch thereof. They are

rarely terminal especially on serum (fig. 14 or 21), similar to those figured by Roger ('96) reproduced by Noisette ('98) for their strains of *S. albicans*.

In cultures our organism differs from *S. albicans* and *S. Braultii* in not forming a pellicle on any liquid media, although it is somewhat closer to the latter in morphology. Mazza & Palamedi report that sugars were not fermented nor gelatine liquefied, while Talice & Mackinnon ('34) and ourselves have found the organism to ferment glucose, fructose, mannose, and maltose, and to liquefy gelatine. It is possible that Mazza & Palamedi did not keep their cultures long enough to observe fermentation or liquefaction. After a study of Mazza & Palamedi's cultures, Talice & Mackinnon have reduced this species to synonymy with *Syringospora albicans* under the synonym *Mycotorula albicans* (Robin) Langeron & Talice. While this organism shows many characters in common with *S. albicans*, its invasive power is so much greater (being severely pathogenic to rabbit after two years in culture) that it hardly seems likely that it is the same as *S. albicans* which is a mild parasite of the mucosa of infants, or of extremely senile or moribund adults, having little or no power to invade the skin or lungs of adults. *S. inexorabilis*, starting in the lungs or buccal mucosa of a healthy farm laborer, produced a generalized infection involving the skin and invading the tissues.

While recognizing that only a thorough monograph along the lines of that undertaken by the Centraalbureau voor Schimmelcultures, but upon a variety of suitable media not used there, can settle the systematic position of these organisms, it seems better to transfer the species to *Syringospora*, where it may be characterized as follows:

SYRINGOSPORA INEXORABILIS (Mazza & Palamedi) Dodge, Med. Myc. 242. 1935.

*Monilia inexorabilis* Mazza & Palamedi, Reunión Soc. Argentina Patol. Reg. del Norte en Tucumán 7: 424-467, 1 pl. 50 fig. 1932.

*Mycotorula albicans* Talice & Mackinnon, Reunión Soc. Argentina Patol. Reg. del Norte, Santiago del Estero 8: 165-166. 1934.

Isolated from blastomycosis of the skin and mucosa of a patient in the Argentine Chaco by Mazza and Palamedi ('32); pathogenic to guinea pig and rabbit. Perhaps the case of Rockwood & Greenwood ('34) should be referred here, although the autopsy findings were less positive.

Yeast cells in tissue and pus, spherical. Yeast cells common in media of low hydrogen-ion concentration and higher oxygen tension, thin-walled except on serum. In higher hydrogen-ion concentrations pseudo-mycelium abundant in favorable media, true mycelium or racquet mycelium in unfavorable media. Blastospores single or in short, branched chains, usually at the septa, occasionally scattered in poor media.

#### RELATED SPECIES

Recently, Ciferri and Redaelli ('35) published notes on the morphology of several species of *Syringospora* and related genera, which had previously been very imperfectly known. As this information was received too late to incorporate in Dodge's 'Medical Mycology' ('35), it seems desirable to summarize it here and record the new combinations made necessary by the new information.

*SYRINGOSPORA dimorpha* (Redaelli & Ciferri) Dodge & Moore, n. comb.

*Mycotorula dimorpha* Redaelli & Ciferri, Arch. Mikrobiol. 6: 43-46, fig. 28, 29. 1935.

*Mycotorula interdigitalis* Redaelli, 1930. non Pollacci & Nannizzi.

Isolated from dysidrosiform lesions of the interdigital spaces of a patient in Cairo, Egypt. (Soliman, strain 3). Pathogenic for guinea pig.

Hyphae long, septate, little-branched, producing dense verticils of blastospores at the septa. Blastospores  $3 \times 3.5 \mu$ .

On glucose agar, colony rounded (3 cm. in 20 days), dense, creamy, dirty white tending toward yellowish, central portion somewhat elevated, broadly crateriform, smooth, with outer 6 mm. next margin grayish, deeply radially furrowed, margin round. On liquid media producing a ring on malt extract,

otherwise with a few floating islets which settle as an abundant floccose sediment. Fermentation of glucose, fructose and mannose, acid with the other carbohydrates. No action on milk; gelatin liquefied within 5 days.

*MYCOTORULOIDES macedoniensis* (Castellani) Dodge & Moore, n. comb.

*Monilia macedoniensis* Castellani & Chalmers, Man. Trop. Med. ed. 3, 1087. 1919.

*Myceloblastanion macedoniense* Ota, Jap. Jour. Derm. Urol. 28: 127. 1928.

*Castellania macedoniensis* Dodge, Med. Myc. 259. 1935.

*Mycotorula macedoniensis* Redaelli & Ciferri in Ciferri & Redaelli, Arch. Mikrobiol. 6: 18. 1935.

Originally isolated from sputum of a patient in Macedonia by Castellani. The culture studied by Ciferri and Redaelli was received from Castellani under the name *Monilia macedoniensis* var. *macedoniensoides* Cast., isolated from sputum. Castellani & Taylor ('25) originally described *Monilia macedoniensoides* in a paper on vaginal monilias, and while they do not specifically state that this species came from the vagina one would assume that such is the case. Later the same year, Castellani, Douglas & Thompson ('25) list it in a paper on infections of the bronchi without giving data as to its origin. Ashford ('31) studied two strains of this species from Castellani, reporting glucose and fructose fermented by both strains; maltose, sucrose, galactose, and inulin fermented by one strain which fermented maltose only once in nine sowings. Acid was produced with glucose, maltose, galactose, xylose; about half the time with lactose and raffinose; and about one-fourth the time with mannitol and dextrin.

On liquid media only the yeast stage of ovoid cells  $3-4 \times 4.5-5 \mu$ , budding monopolar, rarely bipolar, rarely in short chains but no true filaments. On solid media (Difco nutrient agar with glucose) hyphae with verticils of blastospores at the septa. From Ciferri and Redaelli's illustrations, hyphae rarely branched, blastospores usually in compact verticils, occasionally in short, branched chains characteristic of *Myco-*

*toruloides* Lang. & Tal. Blastospores evidently variable, but no dimensions or magnifications of figures given.

Giant colony after 15 days in Difco nutrient agar with glucose at room temperatures, circular, 1 cm. in diameter, creamy white, smooth, shining, center slightly elevated, smooth, sloping gradually to the periphery with rare radial folds, margin smooth, thin, uniform or finally mammillate. Sanfilippo ('24), who studied Castellani's culture, reports sediment in broth; no turbidity nor pellicle.

Fermentation and acid production in glucose, fructose, galactose, sucrose, and inulin; milk coagulated; gelatin and serum not liquefied.

From both its morphology and biochemical characters this species seems to belong to *Mycotoruloides*, although the younger hyphae are suggestive of *Syringospora*. Var. *macedoniensisoides* differs only in not coagulating milk.

*MYCOTORULOIDES trimorpha* (Redaelli & Ciferri) Dodge & Moore, n. comb.

*Mycotorula trimorpha* Redaelli & Ciferri, Arch. Mikrobiol. 6: 35. 1935.

*Candida insolita* Redaelli in Graziano, Giorn. Batt. Immun. 5: 1070-1075. 1 fig. 1933. non (Cast.) Basgal, Contr. Estudo Blastomycoses Pulmonares, p. 49. 1931.

Isolated from feces in cases of enteritis of infants by Graziano ('33). Not pathogenic for guinea pig.

In solid media only yeast cells present. In liquid cultures, hyphae long, little-branched, of long cells bearing dense verticils at the septa, blastospores of the verticils in short-branched chains,  $2.4\ \mu$  in diameter with a large hyaline cell (chlamydo-spore) at the tip of the hyphae up to  $10\ \mu$  in diameter. Under some conditions these may proliferate to 8-10 cells in a chain, suggesting the condition found in *Monilia*.

On Sabouraud, carrot, and malt-extract agars, colony smooth, white, creamy, margin smooth, surface shining; on malt, carrot and potato, medium colored yellow. On gelatin colonies color similar but opaque, penetrating somewhat into the medium. In carrot decoction and malt extract, complete

ring and incomplete thin pellicle, abundant sediment, and slight turbidity.

Obligate aerobe, optimum temperature 37° C., growth good but much slower at room temperature. Ferments glucose, fructose, maltose, galactose, and sucrose; slight acid production on most media; milk not coagulated nor digested; gelatin and serum not liquefied.

*PARENDOMYCES Flareri* (Redaelli & Ciferri) Dodge & Moore, n. comb.

*Blastodendrion Flareri* Redaelli & Ciferri, Arch. Mikrobiol. 6: 51-53, fig. 35, 36. 1935.

Strain 2 Cazzani was isolated by Flarer from scaling erythematous lesion of the human skin, and Strain 8 from an eczematous lesion, both in Messina, Italy. Not found pathogenic for guinea pig by intravenous injection.

Cells sprouting, forming small branched groups, rarely short, highly branched filaments, of blastospores variable in shape and size,  $1.5-2.3 \times 2-3 \mu$ ; chlamydospores  $5 \mu$  in diameter; cells filled with dense homogeneous protoplasm or uniguttulate except in old vacuolate cells.

On Sabouraud agar, colony round, dense, creamy, white, center elevated, slightly crateriform, sloping gently to the smooth margin, surface rather dull. In liquid media only an incomplete ring, with discrete sediment of conglutinate floccose colonies; in some media with a diffuse opalescence. No fermentation of carbohydrates; acid in dextrose, levulose, and mannose; no action on milk, nor on gelatine. Strain 8 also produced acid in galactose and raffinose.

Apparently differs from *P. Perryi* (Castellani) Dodge, in not producing acid on maltose.

*PSEUDOMONILIA verticillata* (Redaelli & Ciferri) Dodge & Moore, n. comb.

*Mycotorula verticillata* Redaelli & Ciferri, Arch. Mikrobiol. 6: 40. 1935.

Isolated at Milan, Italy, from a scaling erythematous lesion of the skin. Pathogenic for guinea pig.



Hyphae branched with verticils at the septa, verticils often of only two cells. Occasionally tufts of mycelium rise above the colony when the verticils are denser, suggesting *Syringospora*; blastospores ovoid to spherical, about  $3.5\ \mu$  in diameter.

On glucose agar, colony irregularly rounded, much elevated above the substrate (10–12 mm. in diameter in 20 days at room temperature), shining, whitish, opaque, cerebriform, irregular, marginal lobes smooth and thick. On liquid media, a ring with confluent islets forming a pellicle and abundant sediment. No fermentation of sugars; acid in glucose, mannose, fructose, galactose, and maltose; no action on milk or gelatin.

From its biochemical characters this species seems to belong rather to *Pseudomonilia* than to *Syringospora* (*Mycotorula* Lang. & Tal.). Morphologically the aerial mycelium sometimes suggests the latter, although in liquid media and within the colony it is typical of *Pseudomonilia*.

*PSEUDOMONILIA zeylanoides* (Shaw) Dodge & Moore, n. comb.

*Monilia zeylanoides* Shaw, Centralbl. f. Bakt. I. 119: 460–464. 1931. non Cast.

*Mycotorula zeylanoides* Redaelli & Ciferri, Arch. Mikrobiol. 6: 41–43, fig. 26, 27. 1935.

Isolated by Shaw from sputum and referred to *Monilia zeylanoides* Cast in 1931. Isolated by Carco from tonsillar lesions with the usual symptoms of a mycosis.

Hyphae long, hyaline, septate, with moderate branching, blastospores in reduced verticils at the septa.

On solid media colony dense, yellowish-white, becoming intense yellow in age, surface shining, margin smooth at first, becoming fringed. Giant colony showing three zones, center somewhat elevated and crateriform, second irregularly hilly suggesting lava flows, dense, milk-white, outer zone creamy color, thinner, opaque, finely fringed. On liquid media, complete ring, tough, dense, white, also thin pellicle of coalescing islets with abundant sediment. No fermentation of sugars; acid in glucose, fructose, mannose, galactose, maltose, inulin, and xylose; no action on milk; gelatin not liquefied.

This species differs from *Parendomyces zeylanoides* (Cast.) Dodge, to which it was referred by Shaw, in not coagulating milk, and in its abundant hyphae. It seems more closely related to *Pseudomonilia matalensis* (Cast.) Dodge, from which it differs in the thinner white pellicle and abundant sediment in liquid media, and the production of acid in most sugars, acid production in *P. matalensis* being slight or none.

**MYCODERMA desidiosum** (Ciferri & Redaelli) Dodge & Moore, n. comb.

*Candida desidiosa* Ciferri & Redaelli, Arch. Mikrobiol. 6: 62-64. 1935.

Isolated from the intestinal contents of pigeons with experimental beriberi along with *Candida Krusei*. Pathogenic for guinea pigs.

Mycelium of short ellipsoidal blastospores, somewhat branched, cells filled with oil droplets.

On glucose agar, colony round, 1.5 cm. in diameter, cream to yellowish, dense, shining, central portion irregularly rounded, elevated but flat, smooth, with a few slight hillocks at the center; outer slope steep to margin which is smooth or slightly and indistinctly mammillate. In age, a slight grayish halo with a finely plumose margin so that three zones appear; a central plateau, an irregular mammillate, smooth, shining white zone, and a very thin grayish plumose margin. On liquid media, ring incomplete, better developed and yellowish on malt extract, slight turbidity, sediment in a single conglutinate mass. No fermentation.

**CANDIDA dendritica** (Ciferri & Redaelli) Dodge & Moore, n. comb.

*Trichosporon (Geotrichoides) dendriticum* Ciferri & Redaelli, Arch. Mikrobiol. 6: 53-58, fig. 37-38. 1935.

Isolated along with *Blastodendron Pinoyi* (Cast.) Lang & Tal. from a patient with bronchomoniliasis in Milan, Italy. Pathogenicity not stated.

Mycelium 1.5-2.3  $\mu$  in diameter, somewhat verticillately branched. Arthrospores abundant, 2.3-2.5  $\times$  7-9  $\mu$ ; blasto-

spores rare, ellipsoidal, tending to occur in verticils as in *Syringospora*.

On glucose agar, central portion whitish, creamy, mycelium mostly submerged in dendritic fascicles, with a thin, branched plumose margin. In liquid media a thin pellicle within 24 hours. Glucose and fructose fermented.

This species has been too imperfectly described for certain systematic position, but since *Trichosporon* is held to be untenable as a generic name, it seems best to place it here, pending further study.

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## EXPLANATION OF PLATE

## PLATE 15

*Syringospora inexorabilis* (*Monilia inexorabilis*)

All figures drawn with the aid of a camera lucida at a magnification of  $\times 1440$  and reduced to  $\times 765$ .

Figs. 1-6. Cells developing from blastospore or yeast-like cell.

Fig. 7. Collar-like cross-wall on Endo's agar.

Fig. 8. Type of mycelium on Czapek's agar.

Fig. 9. Group of budding yeast-like cells on malt extract agar.

Fig. 10. Type of mycelium with blastospores, on lactose agar.

Fig. 11. Type of mycelium on yeast-dextrose agar.

Fig. 12. Giant, spherical thick-walled cells on wort agar.

Fig. 13. Cells on wort agar.

Fig. 14. Type of cells in serum.

Fig. 15. Cells on yeast-dextrose agar.

Figs. 16-17. Type of mycelium on Raulin's solution.

Fig. 18. Blastospores on Czapek's agar.

Fig. 19. Mycelium with blastospores on Endo's agar.

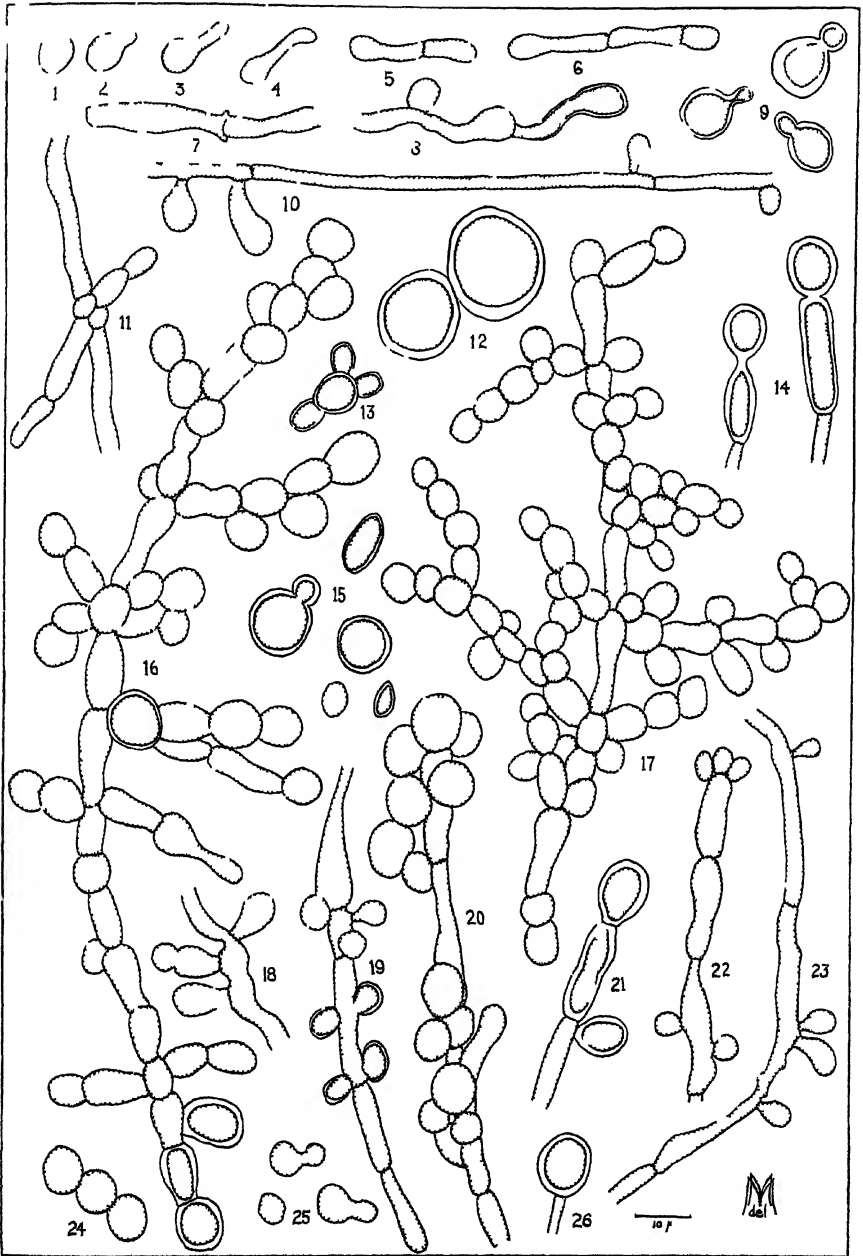
Fig. 20. Mycelium with blastospores on nutrient blood agar.

Fig. 21. Cells in serum.

Figs. 22-23. Mycelium on Endo's agar with peculiar oidoid cells at apex (fig. 22).

Figs. 24-25. Cells on nutrient blood agar.

Fig. 26. Cells in serum.



## EXPLANATION OF PLATE

## PLATE 16

*Synigospora meaeorabilis* (*Monilia metonabitis*)

All figures drawn with the aid of a camera lucida. Figs. 27-50 drawn at a magnification of  $\times 2300$  and reduced to  $\times 1220$ . Figs. 51-55 drawn at a magnification of  $\times 1440$  and reduced to  $\times 765$ .

Figs. 27-29. Uninucleate cells showing metachromatic material in cytoplasm and nucleoplasm.

Fig. 30. Cell showing elongation and early contraction of walls.

Fig. 31. Elongated cell showing early concentration of nucleoplasmic granules at opposite ends of nucleus.

Fig. 32. Early stage in division of nucleus with concentration of metachromatic material.

Fig. 33. Showing a divided nucleus and an elongated nucleus ready for division.

Fig. 34. Nucleus prior to concentration of metachromatic material.

Fig. 35. Nucleus which is to divide by transverse abscission of cell.

Fig. 36. Budding cell with dividing nucleus.

Fig. 37. Budding cell with divided nucleus. A daughter nucleus will migrate into the bud.

Fig. 38. Apical cell showing transverse abscission and division of nucleus.

Fig. 39. Cell ready to divide, with nuclei at opposite ends.

Fig. 40. Large budding yeast like cell prior to division of nucleus.

Figs. 41-42. Budding yeast-like cells with nuclei pushing into buds.

Fig. 43. Yeast-like cell which has budded and divided the nucleus amitotically.

Fig. 44. Early stage in transverse abscission of cell and nucleus.

Fig. 45. Group of cells showing nuclei at point of contact.

Fig. 46. Group of cells ready to divide as fig. 39.

Fig. 47. Elongated, narrow hyphae showing blastospores and centrally located, elongated nuclei in filament.

Figs. 48-50. Mycelium showing budding blastospores and dividing nuclei in various stages of development.

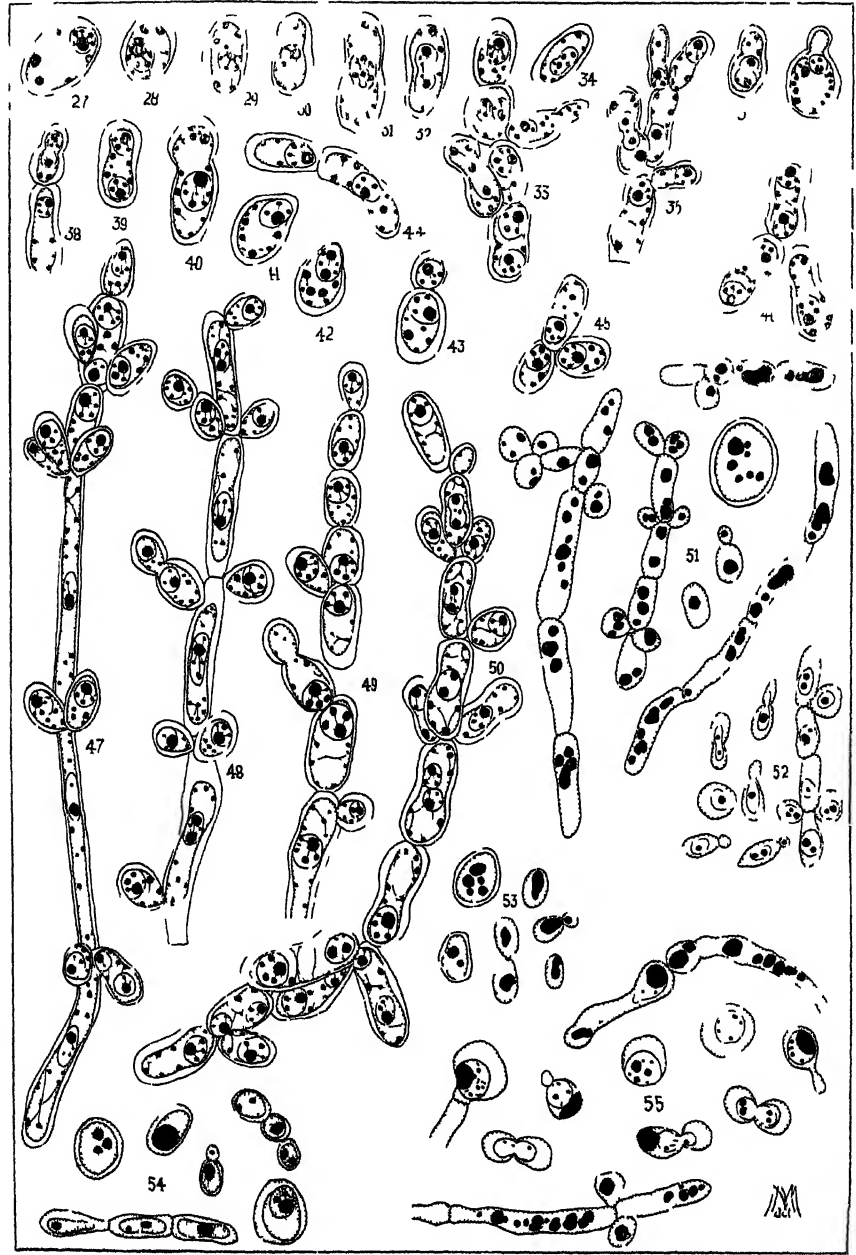
Fig. 51. Mycelium mounted in 2 per cent osmic acid, showing fat globules.

Fig. 52. Mycelium mounted in distilled water with a pinch of benzidine sulphate, showing vacuoles and "dancing bodies."

Fig. 53. Mycelium mounted in 5 per cent platinum chloride, showing the same picture as with osmic acid.

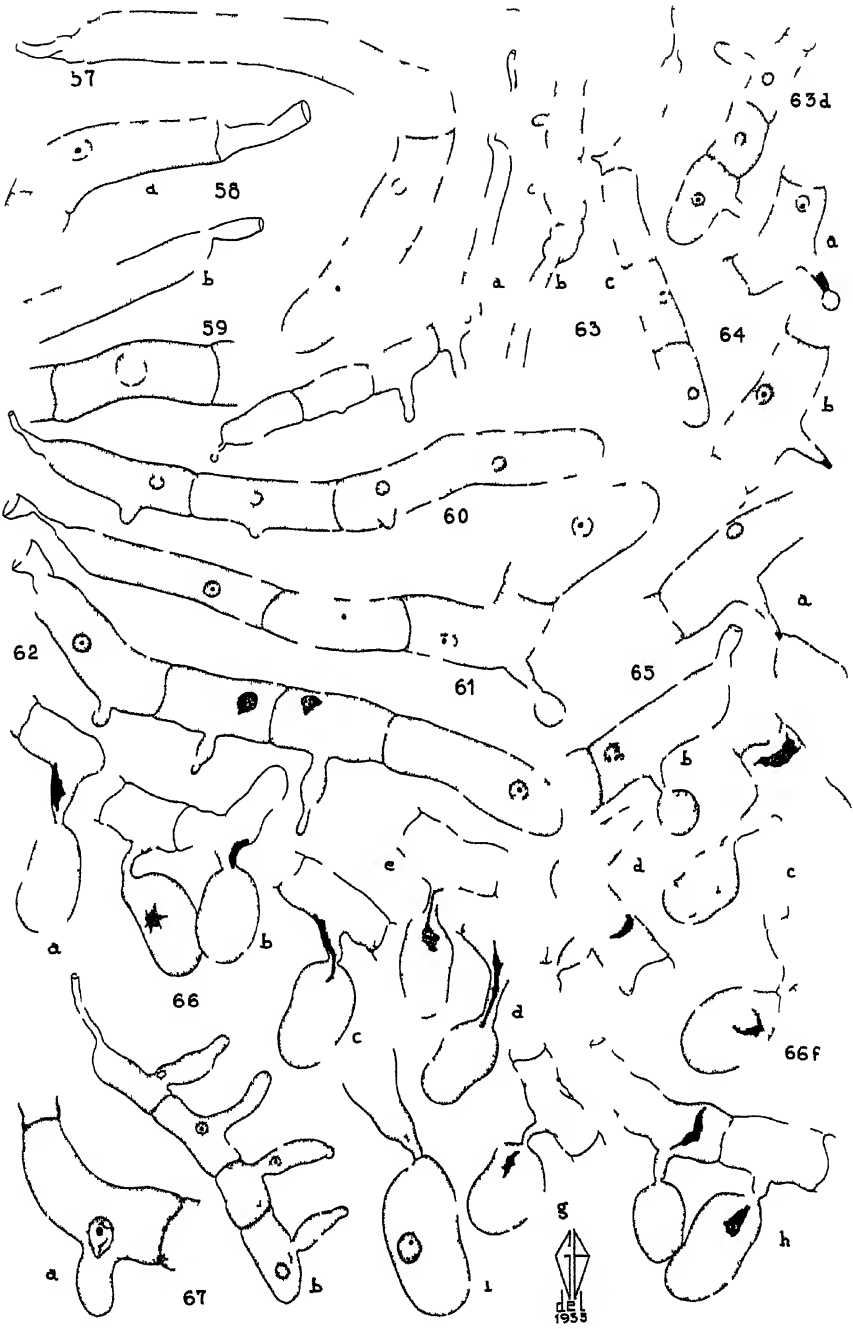
Fig. 54. Mycelium mounted in 1 per cent aqueous methylene blue, showing precipitated volutin.

Fig. 55. Mycelium mounted in saturated iodine potassium iodide, showing glycogen as dark globules, fat and lipoidal substances as small refractile bodies, and possible chondriosomes as short rods.











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## TRANSITIONAL PITTING IN TRACHEIDS OF PSILOTUM

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Most of the anatomical studies upon *Psilotum* have been in connection with the interpretation of the spore-bearing structures and with the general organization of the stele. Accounts of the anatomical organization of the axis have been largely topographical, discussing the distribution of the cortical tissues and the differentiation of the stelar tissues, principally as seen in cross-section (Bertrand, '85, Boodle, '04, Ford, '04, Stiles, '10). The position and order of development of the wood elements have been very definitely emphasized, whereas the nature of the elements themselves has scarcely been more than mentioned. It has been stated generally that the protoxylem elements are spiral tracheids, and that the metaxylem elements are scalariform or somewhat reticulate tracheids.

Previous anatomical studies have furnished two illustrations of pitting types in the tracheids of *Psilotum*. Bertrand ('85) illustrated diagrammatically several types of tracheids which he had seen in longitudinal section in the stele of the subterranean axis. In the accompanying text he described spiral protoxylem elements and scalariform metaxylem elements with

areolate pits. Boodle ('04) illustrated secondary tracheids having irregular or scalariform pitting.

In other groups of vascular plants, the development of secondary thickening types in the maturation of the primary xylem has been regarded as fundamental recapitulatory evidence of evolution. In *Psilotum*, a simple modern vascular plant that in many respects seems to hark back to the Palaeozoic for its hypothetical ancestors, a knowledge of the type of transitional pitting would be fundamentally important in determining more closely the exact phylogenetic status of the plant.

We have studied material of *Psilotum nudum* (L.) Gris. (*P. triquetrum* Sw.), which was obtained from living plants in the collection of the Missouri Botanical Garden at St. Louis. Pieces of the aerial axis were killed in formalin-acetic-alcohol, embedded in paraffin, and cut into serial longitudinal sections 10  $\mu$  thick with a rotary microtome. The sections were stained with Safranin and Fast Green FCF and photographed on Wratten M plates, using a Wratten G filter with a photoflood light.

The transition in types of secondary thickening of the xylem of *Psilotum*, passing from the protoxylem to the metaxylem, is similar to that described by Bailey ('25) as occurring in various groups of Pteropsids. Due to the small size of the actinostele in *Psilotum*, only a few cells are involved. Consequently the transition is more abrupt than that which is found in more advanced groups. In spite of the fact that only a few cells are involved, there has been observed practically every transition type that has been found in the gymnosperms.

The first formed protoxylem elements invariably are provided with loosely wound spiral or annular secondary thickenings (pl. 17, figs. 1, 7; pl. 18, fig. 9). In the succeeding exarch development of tracheids, the secondary thickening generally forms an irregular reticulate structure (figs. 7, 9). From this stage on, the formation of scalariform pits (fig. 10), of somewhat elongate bordered pits, and of true circular bordered pits is usually observed. The transition seems to follow along a

number of separate lines of specialization which depend in part on the size of the elements involved. The web-like structure may give rise to more or less regular alternately arranged bordered pits (figs. 3, 4, 9), with occasional opposite pits (fig. 4), which are apparently due to irregularities in the net. In smaller cells, or those in which the secondary thickening does not assume the net structure, typical uniseriate bordered pits may be formed (fig. 1). These may be close together (araucarian) or widely spaced (abietinean).

Typical annular or scalariform thickenings (figs. 5, 6, 10) may break up to form circular bordered pits. That we are dealing with true bordered pits seems quite obvious. The overhanging thickenings forming the "dome-like" border of the pits are clearly seen in figs. 8 and 11. We have observed no thickening of the primary wall (torus) in connection with these pits.

It has been conjectured that *Psilotum* may be an extremely ancient plant which has come down through time relatively unchanged morphologically from its psilopsid ancestors, or that *Psilotum* may represent a group of plants once quite complex, but now through reduction become rather simple morphologically (Zimmermann, '30).

The display of transitional pitting seems to us to be of considerable phylogenetic significance. A general type of transition from spiral protoxylem to more definite types of metaxylem pitting has been observed in most large groups of Pteropsida (Bailey, '25). If this uniformity occurred consistently in all groups, such transition would lose significance, but, inasmuch as it is unreported in the Psilophytales, that fact seems to have specific bearing on the relation of *Psilotum* and that group.

Apparently the wood of the Psilophytales showed only annular and spiral thickenings. Kidston and Lang ('20) state definitely that they found no trace of any scalariform or pitted tracheids in the Devonian plants they studied. In *Baragwanathia longifolia*, a vascular plant of Silurian age, only ring-like secondary thickenings have been seen (Lang and Cookson, '35). In other respects the general morphology of *Psilotum* is dis-

tinctly not far removed from that of the primitive Devonian plants. It is not difficult to conceive that during the progress of their evolution these Devonian plants gave rise to *Psilotum* with its advanced stelar anatomy, and otherwise morphologically underwent little change.

If *Psilotum* approaches the simple Devonian plants by reason of reduction, one simply infers that the pit transition is vestigial. In the extreme, this line of thought might be considered to show that *Psilotum* represents a phylum of vascular plants, perhaps unrelated to the Psilophytales, in which bordered pits had evolved with or even preceding scalariform types. Then, such a series of transitional stages might be taken to mean that *Psilotum* is a greatly reduced form. Boodle ('04) has suggested that the secondary xylem which he observed in the axis indicated the possibility of origin from the type of *Sphenophyllum* or some Lycopsid.

Unless pitting types, such as we have demonstrated in *Psilotum*, at some future time are found in the simpler Devonian plants, the evidence seems to suggest strongly that *Psilotum* is more highly evolved with respect to these characters than are the Psilophytales.

For the drawings we are indebted to Dr. Gladys E. Baker.

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## EXPLANATION OF PLATE

## PLATE 17

Photomicrographs of types of secondary wall thickening and pitting in xylem of *Psilotum*.

Fig. 1. Elements with loose spiral, spiral thickenings, and bordered pits.

Fig. 2. Elements with annular, reticulate and spiral thickenings.

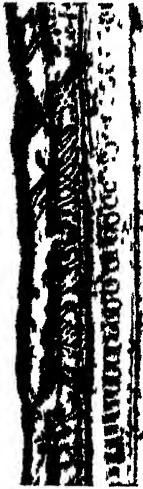
Figs. 3 and 4. Transition from elongate scalariform bordered pits to alternate biseriate bordered pits.

Fig. 5. Typical scalariform metaxylem thickening.

Fig. 6. Elongate bordered pits.

Fig. 7. Spiral thickenings and transition from spiral to reticulate structure.

Fig. 8. Section of tracheid wall showing overarching walls of the bordered pit-pairs.



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MOORE AND ANDREWS—TRACHEIDS OF PSILOTUM

## EXPLANATION OF PLATE

## PLATE 18

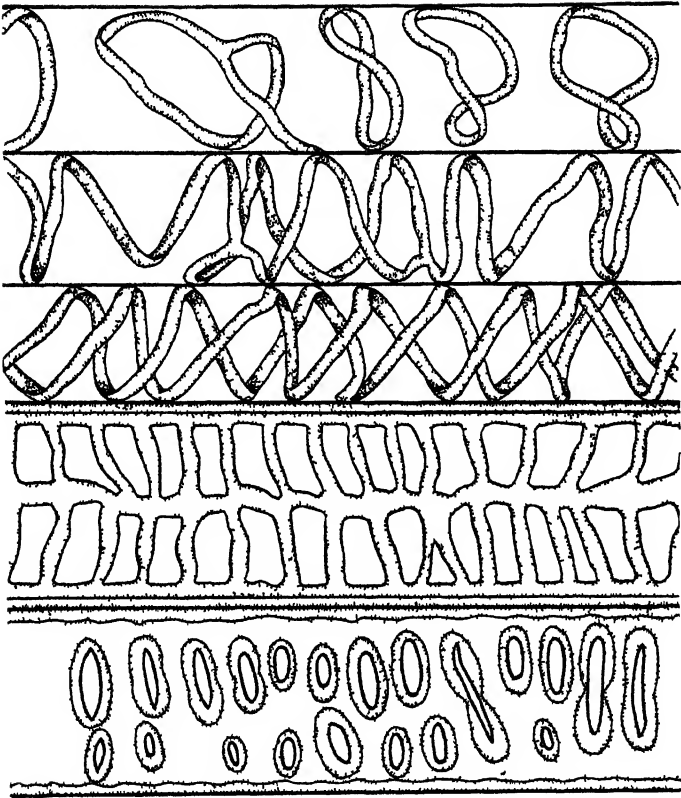
Camera lucida drawings of tracheids of *Psilotum*.

Fig. 9. Transition stages in development of secondary thickenings from irregular ring spinals to irregular reticulations to scalariform bordered pits.

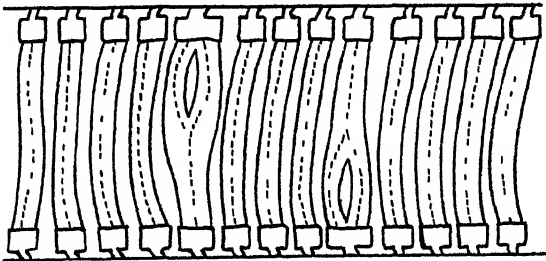
Fig. 10. Scalariform element showing development of occasional bordered pits.

Fig. 11. Structure of bordered pits as seen in longitudinal section.

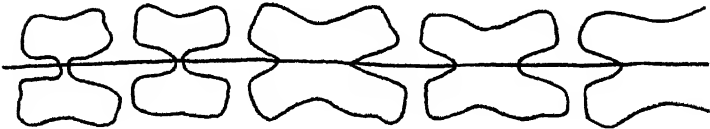
9  
MOORE AND ANDREWS—TRACHEIDS OF PSILLOTUM



10



11





# AN EXPERIMENTAL STUDY OF HYBRIDIZATION IN THE GENUS APOCYNUM

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## INTRODUCTION

In his monograph of the genus *Apocynum*, Woodson ('30) maintained a rather extreme position as to the prevalence and importance of interspecific hybridization in that genus. He classified the Apocynums of eastern North America in four species, *A. hypericifolium*, *A. cannabinum*, *A. androsaemifolium*, and *A. medium*, the last derived from hybridization between two of the others. The remaining variants, largely (according to Woodson) the result of hybridization, were allocated to some 14 varieties of these major species. Figure 2, a copy of his fig. 11, presents a graphical summary of his hypotheses as to phylogenetic relationships in the genus. To the writer these ideas, though stimulating and interesting, seemed rather in need of experimental confirmation by other than purely morphological criteria. After much friendly argument an experiment was planned and carried to completion in the experimental grounds of the Bussey Institution of Harvard University. It consisted in making progeny tests of individual plants of *Apocynum cannabinum* and *A. androsaemifolium*, and their suspected hybrid, *A. medium*. It is pleasant to report that the genetical and cytological data not only confirmed Dr. Woodson's general thesis but that they agreed exactly with several minor details of his hypothesis about which the writer had been extremely skeptical.

*Methods.*—Seed of *Apocynum medium* and *A. cannabinum* was collected by Dr. R. E. Woodson in a field near South Bend, Indiana, where *A. cannabinum* grows in company with a lesser number of *A. androsaemifolium* and their putative hybrid, *A. medium*. Seed was collected from five different plants of *A.*

*medium* and from one plant of *A. cannabinum*, the seeds from each plant being kept separate. The writer collected seeds of *A. androsaemifolium* from one of several plants growing in a meadow on the banks of the Concord River near Billerica, Massachusetts. They were sown in the greenhouse in the winter of 1934 and the resulting seedlings planted out the following spring. During the summer of 1935, when they were a year and a half old and fully mature, they were kept under careful observation by the writer. To reduce the personal equation to a minimum, counts of pollen fertility were made by Mr. Lawrence Regan, who was completely unacquainted with the history of the plants he was examining. The taxonomic determination of the progeny was equally objective. A com-

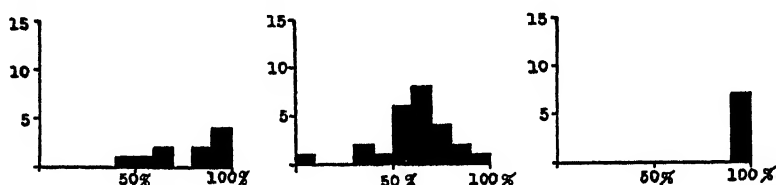


Fig. 1. *A. androsaemifolium* (left), *A. medium* (center), and *A. cannabinum* (right). Horizontal axis represents per cent of fertile pollen, vertical axis, number of individuals.

prehensive flowering and fruiting herbarium specimen was made of nearly every plant. Each was tagged with a serial number, and the specimens, completely shuffled, were handed over to Dr. Woodson for identification. To increase the objectivity he was not even informed as to the source or the specific identity or the relative amount of material grown from seed collected by the writer. The data as presented below are therefore unusually trustworthy, even for a scientific experiment.

The results of the progeny test are presented in full in table I and certain points are summarized in fig. 1. The progeny of each plant are listed together; for each seedling the table gives the individual record number, the percentage of fertile pollen as determined by Mr. Regan, and its probable specific identity as determined by Dr. Woodson from the herbarium specimen

submitted to him. His comments have been added in the last column since they have a direct bearing upon the problem.

### CONCLUSIONS

1. *Pollen fertility*.—The progeny of *Apocynum cannabinum* had pollen of uniformly high fertility. Those of *A. androsaemifolium* were mostly of high fertility though a few seedlings were semi-sterile. The progeny of *A. medium* were characterized by a low average fertility. The results are presented graphically in fig. 1.

2. *Genetical results*.—The putative parental species, *A. cannabinum* and *A. androsaemifolium*, both bred true, though both segregated noticeably for presence or absence of pubescence. In spite of the small numbers of seedlings obtained, *A. medium* failed to breed true. Of the twenty-six seedlings of *A. medium* pressed and turned over to Dr. Woodson, eighteen were diagnosed as *A. medium*, six as *A. androsaemifolium*, and two as *A. cannabinum*. It is also significant that all the plants about whose absolute specific identity Dr. Woodson had some doubt were among these seedlings of *A. medium*. The comments in the right-hand column of table 1 give a very true picture of the comparative variability of the progeny of *A. cannabinum* and *A. androsaemifolium*, on the one hand, and of *A. medium*, on the other.

3. *Apocynum medium*.—This species is therefore most certainly a hybrid and might well be designated as such in botanical literature. In addition to the evidence which originally led Woodson ('30) to that conclusion, the above experiment has demonstrated that, like most hybrids, it produces variable progeny of low average fertility. Some of these progeny resemble the putative parental species so strongly that in the absence of any information as to their source, they would unhesitatingly be so identified by any one familiar with the species in question.

4. *Apocynum cannabinum* and *A. androsaemifolium*.—These are probably more or less self-sterile as Woodson had already suspected ('30). The existence of as much variation as was



TABLE I

RESULTS OF PROGENY TESTS OF ONE PLANT OF *APOCYNUM CANNABINUM*, ONE OF *A. ANDROSAEMIFOLIUM*, AND FIVE OF *A. MEDIUM*  
(Further explanation in the text)

	Seed- ling No.	Per cent fertile pollen	Identification	Remarks
<i>A. cannabinum</i> No. 447—South Bend, Ind.	1	95	<i>A. cannabinum</i> var. <i>typicum</i>	
	2	93	<i>A. cannabinum</i> var. <i>typicum</i>	
	3	91	<i>A. cannabinum</i> var. <i>glaberrimum</i>	
	4	98	<i>A. cannabinum</i> var. <i>glaberrimum</i>	
	5	98	<i>A. cannabinum</i> var. <i>typicum</i>	
	6	97	<i>A. cannabinum</i> var. <i>typicum</i>	
	7	94	<i>A. cannabinum</i> var. <i>glaberrimum</i>	
<i>A. androsaemifolium</i> No. 503—Billerica, Mass.	1	60		Specimen lost
	2	89	<i>A. androsaemifolium</i>	Very typical
	3	42	<i>A. androsaemifolium</i>	
	4	99	<i>A. androsaemifolium</i>	Fairly typical
	5	86	<i>A. androsaemifolium</i>	
	6	96	<i>A. androsaemifolium</i>	Essentially typical
	7	95	<i>A. androsaemifolium</i>	Very typical
	8	95	<i>A. androsaemifolium</i>	Typical
	9	95		Specimen lost
	10	64	<i>A. androsaemifolium</i>	
	11	68		Specimen lost
<i>A. medium</i> No. 446—South Bend, Ind.	1	89	<i>A. medium</i>	Glabrous leaves
	2	63	<i>A. medium?</i>	Like a small <i>A. androsaemifolium</i>
	3	57	<i>A. medium</i>	Glabrous
	4	64	<i>A. medium</i>	Close to var. <i>leuconeuron</i>
	5	68	<i>A. medium</i>	Sparsely pubescent
	6	64	<i>A. medium</i>	Sparsely pubescent
	7	39	<i>A. medium</i>	Glabrous
	8	72	<i>A. medium</i>	Glabrous
	9	55	<i>A. medium</i>	Glabrous
	10	63	<i>A. medium?</i>	Unusually small
	11	99	<i>A. cannabinum</i> var. <i>glaberrimum</i>	flowers
No. 448—South Bend, Ind.	1	61	Probably a glabrous <i>A. medium</i>	
	2	77	<i>A. medium</i>	

TABLE I—(Continued)

RESULTS OF PROGENY TESTS OF ONE PLANT OF *APOCYNUM CANNABINUM*, ONE OF *A. ANDROSAEMIFOLIUM*, AND FIVE OF *A. MEDIUM*  
(Further explanation in the text)

	Seed- ling No.	Per cent fertile pollen	Identification	Remarks
<i>A. medium</i> (Cont.) No. 449—South Bend, Ind.	1	77	<i>A. medium</i>	But very small flowers
	2	53	<i>A. medium</i>	Quite typical
	3	78	<i>A. medium</i>	But nearly glabrous
	4	93	<i>A. androsaemifolium</i>	
	5	98	<i>A. medium</i>	
No. 502—South Bend, Ind.	1	90	<i>A. cannabinum</i> var. <i>glaberrimum</i> ?	
	2	65	<i>A. androsaemifolium</i>	But small-flowered
No. 504—South Bend, Ind.	1	58	<i>A. medium</i> ?	
	2	37	<i>A. androsaemifolium</i> ?	Possibly a hybrid
	3	41	<i>A. medium</i>	
	4	4	<i>A. androsaemifolium</i>	
	5	57	<i>A. androsaemifolium</i> ?	Corolla rather small

exhibited between sister plants of either species indicates that intra-specific cross-pollinations must be frequent (Anderson, '28). G. Medwedewa has recently shown ('35) for *Apocynum venetum* that pollen-tubes may reach the ovary after self-pollination. She explains the lack of seed obtained in experimental selfings as due to the fact that flowers isolated in paper bags were inundated by their own nectar. There are, however, other mechanisms for self-sterility beside differential pollen-tube growth as has been shown by Stout and Chandler ('33) and others. Medwedewa's demonstration of the superior accelerating effect of foreign stigmas as compared to those from the same plant may be an indication of a deep-seated incompatibility which allows pollen-tube growth in the style but either prevents fertilization or the development of self-fertilized zygotes. As Medwedewa has suggested (loc. cit.), precise genetical tests of vicinism are really necessary for a decisive answer. The results reported above, particularly the progeny test of a plant of *A. androsaemifolium* from Billerica,

bear directly on this point. This plant was not growing in the vicinity of other species of *Apocynum* nor was there any indication of hybridity in the colony, and yet there was marked variation between its progeny. This would indicate a high percentage of out-crossing.

### DISCUSSION

No one doubts any longer that inter-specific hybridization can take place in nature. There remain the determination of its comparative frequency, its taxonomic importance, and its phylogenetic consequences. The evidence reported above suggests that hybridization is of fairly frequent occurrence in the genus, and that it is largely responsible for the taxonomic difficulties encountered in classifying the species of *Apocynum* in eastern North America. These difficulties spring not from the main bulk of the genus, which is readily segregated into the chief species, but from a small percentage of puzzling aberrants. *Apocynum medium* in itself constitutes no great problem in classification, whether it be accepted as a hybrid or maintained as a species. It is rather the small percentage of specimens which are *almost* like typical *A. androsaemifolium*, or *almost* like *A. cannabinum*, or near *A. medium*, which provides a very real problem in classification. Should one deal with these variants as separate species, as was done by the late Edward L. Greene; should one ignore them more or less completely, as have many American botanists; or should one catalogue them as varieties of *A. cannabinum*, *A. androsaemifolium*, and *A. medium*, as was done by Woodson in his monograph? Cogent objections can be raised and have been raised to each of the above procedures. The experiments reported above give little or no information as to the best means of dealing with these puzzling variants; that is of course mainly a problem in classification. On the biological question of their origin and phylogenetic importance the evidence is, however, quite specific. Clearly, if the above results are typical, these variants are secondary hybrids one or more generations removed from the original cross between the species. They may

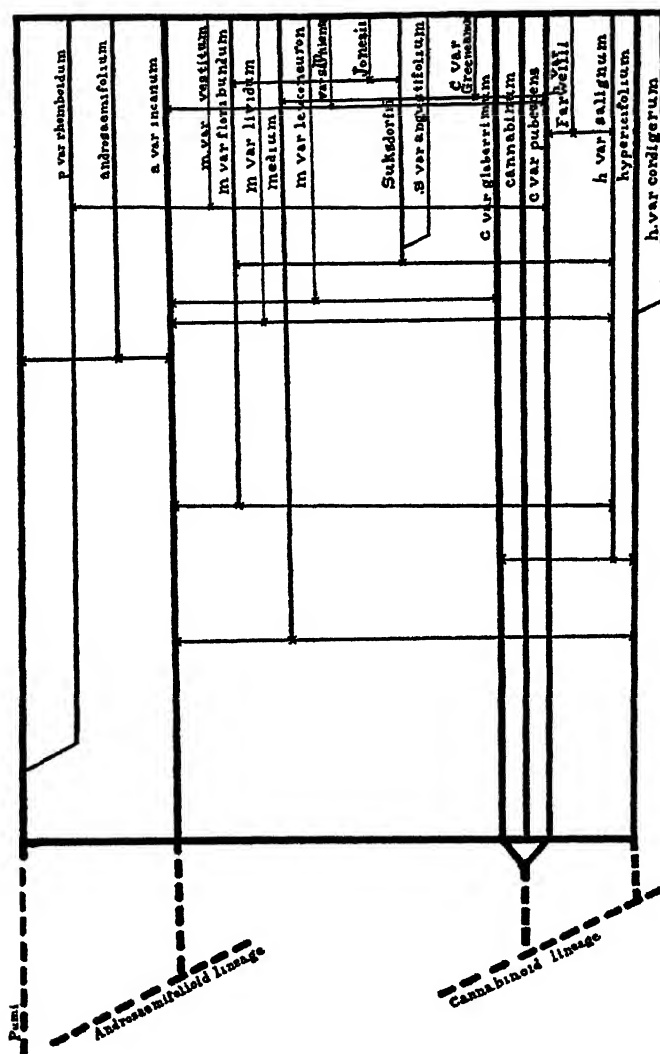


Fig. 2. Phylogenetic relationships of American species of *Apocynum* according to Woodson. Broken lines represent the hypothetical rudiments of the genus, the solid lines, the supposed relationship of the known species and varieties.

Note: According to more recent nomenclatural corrections, "*A. androsaemifolium*" in the chart should read *A. androsaemifolium* var. *glabrum*; and "*A. androsaemifolium* var. *incanum*" should be *A. androsaemifolium*, typical variety (cf. *Rhodora* 34: 30-31. 1932).

be very probably crossed back to one of original parental species, at least in part, and may often resemble that species superficially. It will be remembered that the puzzling seedlings of *A. androsaemifolium* came not directly from that species, but were hybrid segregates closely resembling it. In *Apocynum*, therefore, one of the chief effects of hybridization seems to be the enrichment of the variability of the original species taking part in the hybridization.

The actual creation of a new intermediate species by that process, while certainly a possibility, does not seem to have been effected in the case of *A. medium*. That binomial may be a necessity for purposes of classification, but biologically it is still in a far different status from *A. androsaemifolium* and *A. cannabinum*. To reach that status it would require a period of isolation and the operation of natural selection to remove the variability and the semi-sterility which now characterize it. The behavior of *A. medium* No. 449 and of *A. medium* No. 446 is particularly interesting. The former must apparently have been a first-generation cross, for like such plants it is highly heterozygous. Its progeny (pl. 19, fig. 3) include everything from almost straight *A. cannabinum* to a superficially normal *A. androsaemifolium*. *Apocynum medium* No. 446, on the other hand, bred almost true (pl. 19, fig. 4). Most of its progeny were more or less like itself; in it the *A. medium* type is on the way to becoming stabilized and it probably represents a hybrid of the second generation or later. Given a fair degree of isolation there seems to be no reason why such an intermediate type might not in a comparatively short time reach a specific status comparable to that of *A. cannabinum* or of *A. androsaemifolium*.

#### SUMMARY

1. Progeny tests were made of *Apocynum androsaemifolium*, *A. cannabinum*, and their putative hybrid, *A. medium*.

2. *Apocynum androsaemifolium* and *A. cannabinum* bred true. *A. medium* produced a variable set of seedlings, some of them indistinguishable from *A. androsaemifolium* and *A. cannabinum*.

3. The seedlings of *A. cannabinum* had uniformly high percentages of fertile pollen and those of *A. androsaemifolium* were nearly as fertile. Those of *A. medium* were of low average fertility.

4. It is concluded that *A. medium* is certainly a hybrid.

5. The taxonomic importance and phylogenetic consequences of interspecific hybridization in *Apocynum* are discussed in the light of these results. It is suggested that the chief effect of hybridization in this genus in eastern North America at the present time is to increase variability in the parental species.

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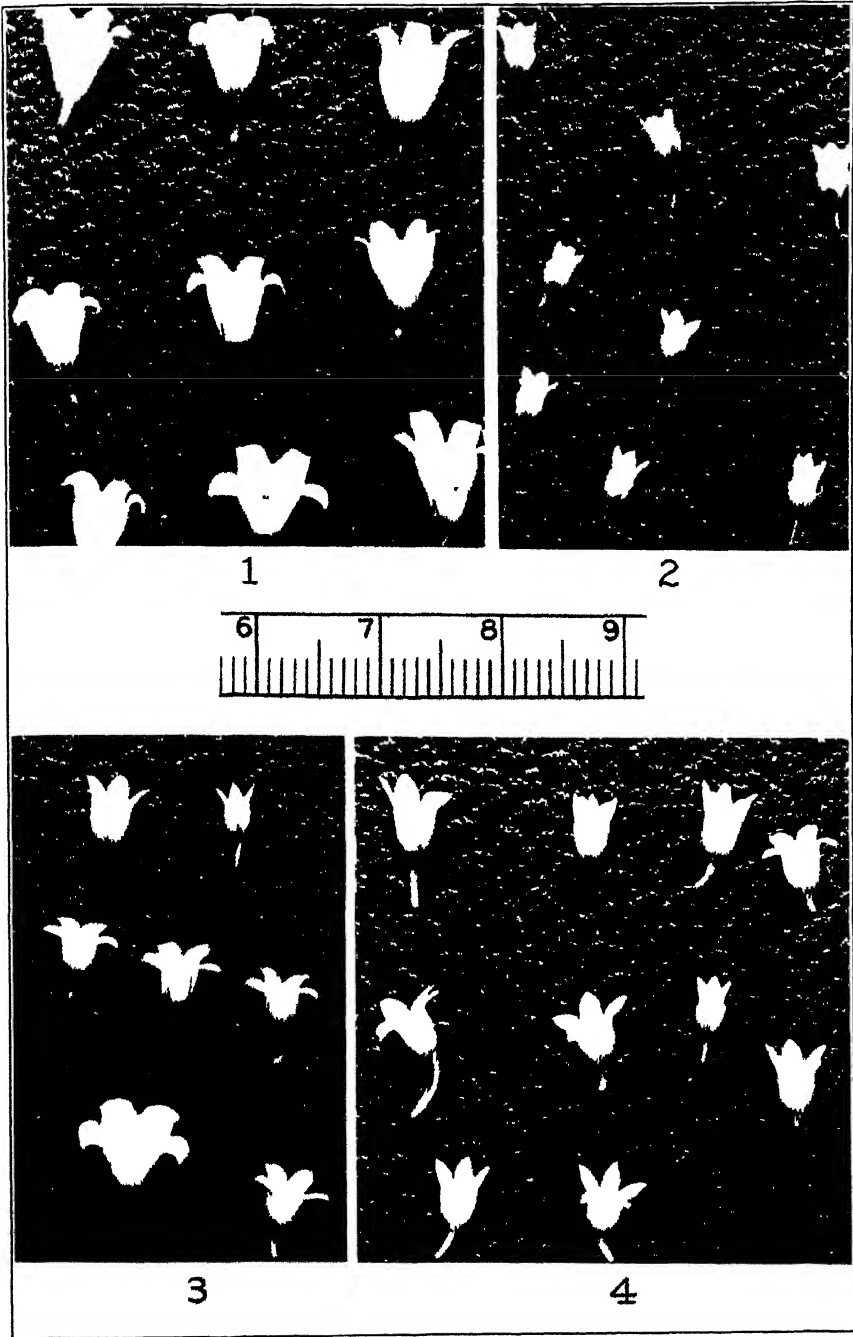
## EXPLANATION OF PLATE

## PLATE 19

Photographs of one flower from each plant for;

- 1, nine seedlings of *A. androsaemifolium* No. 503.
- 2, eight seedlings of *A. cannabinum* No. 447.
- 3, seven seedlings of *A. medium* No. 449.
- 4, ten seedlings of *A. medium* No. 446.

In the center a portion of a centimeter scale photographed at the same magnification for comparison.



ANDERSON--HYBRIDIZATION IN APOCYNUM





# STUDIES IN THE APOCYNACEAE. IV<sup>1</sup>

## THE AMERICAN GENERA OF ECHITOIDEAE

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### X. NEOBRACEA Britton

**Neobracea** Britton, in Britton & Millsp. Bahama Fl. 335. 1920; Urb. Symb. Ant. 9: 240. 1924.

*Bracea* Britton, Bull. N. Y. Bot. Gard. 3: 448. 1905, not King.

Lactescent shrubs or small trees. Stems erect to ascending, terete; branches dichotomous to alternate when adventitious. Leaves opposite, shortly petiolate, penninerved, eglandular, the petioles subtended by 2-several inconspicuous stipular appendages. Inflorescence terminal, less frequently to subterminal or lateral, scorpioidally corymbose to subumbellate, few- to several-flowered, inconspicuously bracteate. Calyx 5-parted, the lobes equal or subequal, cleft nearly to the receptacle, imbricated, eglandular, or bearing within 5-10 alternate squamellae. Corolla infundibuliform, the tube straight, inappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate, or somewhat crescent at the base. Follicles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, truncate, apically comose seeds.

<sup>1</sup> Concluded from ANN. MO. BOT. GARD. 22: 153-306. (187)-(340). 1935.

Issued June 10, 1936.

Type species: *Neobracea bahamensis* Britton, in Britton & Millsp. Bahama Fl. 335. 1920.

#### KEY TO THE SPECIES

- a. Plants glabrous throughout; calyx-lobes rather conspicuously foliaceous, ovate to ovate-oblong; plants of Cuba.....1. *N. Valenzuelana*
- aa. Plants more or less conspicuously pubescent throughout; calyx-lobes scarious or only slightly foliaceous, ovate- to oblong-trigonal.
  - b. Inflorescence corymbose, the peduncle equalling or surpassing the pedicels; plants of Cuba.....2. *N. angustifolia*
  - bb. Inflorescence umbellate or subumbellate, the peduncle markedly shorter than the pedicels.
    - c. Squamellae evident; follicles 15-25 cm. long; plants of the Bahama Islands.....3. *N. bahamensis*
    - cc. Squamellae obsolete or extremely inevident; follicles 5-7 cm. long; plants of Cuba.....4. *N. Ekmanii*

1. *Neobracea Valenzuelana* (A. Rich.) Urb. Symb. Ant. 9: 241. 1924.

*Echites Valenzuelana* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850.

*Rhabdadenia Wrightiana* Muell.-Arg. Linnaea 30: 438. 1860.

*Mandevilla Wrightiana* (Muell.-Arg.) Benth. & Hook. Gen. Pl. 2: 727. 1876.

*Angadenia Valenzuelana* (A. Rich.) Miers, Apoc. So. Am. 181. 1878.

Stems relatively stout, glabrous; leaves opposite, shortly petiolate, obovate to oblong-oblong, apex rounded and usually minutely emarginate, base narrowly cuneate, 2.5-6.0 cm. long, 0.8-2.0 cm. broad, coriaceous, glabrous throughout, dark green, nitidulous above, paler, opaque beneath; petioles 0.5-0.7 cm. long; inflorescence terminal, occasionally pseudo-lateral, subumbellate, bearing 1-5 pale rose flowers; peduncle 0.2-0.8 cm. long; pedicels 2.0-2.5 cm. long, glabrous; bracts 0.2-0.3 cm. long; calyx-lobes ovate to ovate-oblong, obtuse to broadly acute, 0.3-0.5 cm. long, rather conspicuously foliaceous, glabrous, the squamellae in alternate groups of 3-4; corolla infundibuliform, glabrous without, the proper-tube 0.4-0.5 cm. long, about 0.15 cm. in diameter at the base, the

throat broadly conical, 0.8–0.9 cm. long, about 0.6–0.65 cm. in diameter at the orifice, the lobes obliquely obovate-dolabriform, obtuse, 1.4–1.5 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly sagittate, 0.4–0.425 cm. long, minutely tomentulose dorsally; ovary ovoid, about 0.1 cm. long, glabrous; stigma capitate, 0.1 cm. long; nectaries about half equalling the ovary, more or less conspicuously 3-lobed; follicles relatively slender and flexible, very obscurely articulated, 11–15 cm. long, glabrous; seeds 0.7–0.8 cm. long, the very pale, yellowish coma 1.1–1.3 cm. long.

CUBA: ORIENTE: prope Paso Estancia ad Pinales versus in collibus calcareis, May, 1860, *Wright 399* (B, G, MBG, NY, US, V); swampish thicket, alt. 400–500 m., Sierra Nipe, along trail Piedra Gorda to Woodfred, Dec. 8, 1909, *Shafer 1106* (NY); Tiguallillos, Baracoa, Sept. 2, 1917, *Roig 109* (NY); Camp La Gloria, south of Sierra Moa, Dec. 24–30, 1910, *Shafer 8268* (NY); by water, barren savannas, southeast of Holguin, April 9, 1909, *Shafer 1281* (NY); SANTA CLARA: edge of arroyo, palm barren, Santa Clara, April 8–9, 1912, *Britton & Cowell 15290* (NY); palm barren, Motembo, Aug. 10, 1918, *Leon & Roca 8237* (NY); MATANZAS: serpentine hills, near Canasi, Oct. 10, 1927, *Leon 13127* (NY); bushy savanna, San Miguel de los Baños, Aug. 8, 1919, *Leon & Roca 8904* (NY); HABANA: eruptive rock soil, Madruga, March 31, 1903, *Shafer 13* (NY); Baños del Boticario, not far from Campo Florido, July 18, 1912, *Leon 3353* (NY); PINAR DEL RIO: San Jose de Sagua to San Marcos, on serpentine rocks, Jan. 27, 1912, *Shafer 11966* (NY).

The habit of this species varies from that of a shrub to that of a small tree, the height of plants being reported as from 1 to 8 meters. The corolla is white to pinkish, reddish-flushed in the throat. The calyx-lobes, although not large, are rather conspicuously foliaceous, consisting of a definite lamina, in which the midrib is prominent. The spreading position of the calyx-lobes is characteristic.

**2. *Neobracea angustifolia* Britton, Bull. Torrey Bot. Club 53: 462. 1926.**

Stems relatively stout, softly hirsutulose when young, eventually becoming glabrate and inconspicuously lenticellate; leaves opposite, shortly pedicellate, narrowly oblong-elliptic, apex acute to obtuse, base rather narrowly cuneate, 5–7 cm. long, 0.7–1.3 cm. broad, firmly membranaceous, the margins somewhat revolute in desiccation, either surface softly and

rather densely puberulent; petioles 0.3–0.5 cm. long, puberulent; inflorescence lateral, alternate, somewhat shorter than the subtending leaves, bearing 8–20 small, purplish (?) flowers; peduncle minutely puberulent; pedicels 0.45–0.5 cm. long, minutely puberulent; calyx-lobes rather narrowly trigonal, acute to acuminate, 0.2–0.25 cm. long, minutely puberulent without, the solitary, alternate squamellae extremely minute; corolla infundibuliform, minutely and rather sparsely puberulent without, the proper-tube 0.3–0.35 cm. long, about 0.125 cm. in diameter at the base, the throat conical-campanulate, 0.35 cm. long, about 0.4–0.425 cm. in diameter at the orifice, the lobes oblong-dolabriform, obtuse, 0.7–0.725 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers rather narrowly sagittate, 0.325 cm. long, minutely tomentulose dorsally; ovary oblong-ovoid, about 0.1 cm. long, glabrous; stigma subcapitate, about 0.075 cm. long; nectaries compressed-ovoid, about one-third equalling the ovary; follicles unknown.

CUBA: PINAR DEL RIO: rocky soil between Santa Cruz and Las Cayuelas, April 12, 1924, *Boig 3227* (NY, TYPE, MBG, photograph and analytical drawings).

**3. *Neobracea bahamensis* Britton**, in Britton & Millsp. *Bahama Fl.* 335. 1920.

*Bracea bahamensis* Britton, *Bull. N. Y. Bot. Gard.* 3: 448. 1905.

Stems relatively stout, minutely puberulent when young, eventually becoming glabrate; leaves opposite, shortly petiolate, broadly elliptic to oblong-ob lanceolate, apex obtuse to rounded, base more or less narrowly cuneate, 1.5–10.0 cm. long, 0.5–2.5 cm. broad, coriaceous, above yellowish-green, somewhat nitidulous, essentially glabrous, beneath paler, densely and minutely puberulent; petioles 0.2–0.6 cm. long, minutely puberulent; inflorescence terminal, less frequently to subterminal or lateral, umbellate, bearing 1–10 white, reddish-flushed flowers; peduncle 0.4–1.6 cm. long, minutely puberulent; pedicels 0.7–1.5 cm. long, minutely puberulent; bracts very minute, 0.1 cm. or less in length; calyx-lobes trigonal, 0.2–0.3 cm. long, minutely

puberulent without, the squamellae obsolete or extremely in-evident; corolla infundibuliform, minutely puberulent without, the proper-tube 0.15–0.17 cm. long, about 0.1 cm. in diameter at the base, the throat rather narrowly conical, 0.5–0.8 cm. long, about 0.3–0.35 cm. in diameter at the orifice, the lobes obliquely obovate, 1.5–1.8 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly sagittate, 0.35 cm. long, minutely puberulent dorsally; ovary ovoid, about 0.1 cm. long, glabrous; stigma subcapitate, 0.1–0.125 cm. long; nectaries somewhat shorter than the ovary, dentiform; follicles relatively slender and flexile, obscurely and distantly monili-form, 15–25 cm. long, glabrous; seeds 0.45–0.5 cm. long, the pale yellowish coma 1.4–1.5 cm. long.

BAHAMA ISLANDS: New Providence, June 7, 1879, *Brace 493* (NY, TYPE); near Nassau, N. P., April and May, 1903, *Curtiss 137* (MBG, NY); borders of salt marsh, Millers, N. P., Sept. 3, 1904, *Britton & Brace 526* (NY); border of mangrove swamp, Deep Creek, Andros, Aug. 18–Sept. 10, 1906, *Brace 5177* (NY); pineland, near Fresh Creek, Andros, Jan. 28–31, 1910, *Small & Carter 8751* (NY); rocky plain, Orange Creek and vicinity, Cat Island, Febr. 27–28, 1907, *Britton & Millspaugh 5783* (NY); Landrail Point, Crooked Island, Jan. 9–23, 1906, *Brace 4670* (NY); coastal coppice, Pinder's Point, Great Bahama, Febr. 5–13, 1905, *Britton & Millspaugh 3511* (NY); road to South Side, Long Cay, Dec. 7–17, 1905, *Brace 4053* (NY); scrubland, near Georgetown, Great Exuma, Febr. 22–28, 1905, *Britton & Millspaugh 2970* (NY).

#### 4. *Neobracea Ekmanii* Urb. Symb. Ant. 9: 242. 1924.

Stems relatively stout, essentially glabrous; leaves opposite, shortly petiolate, elliptic to elliptic-oblong, apex acute to very obsoletely acuminate, occasionally obtuse, base cuneate, 1–2 cm. long, 0.4–0.8 cm. broad, coriaceous, above essentially glabrous, more or less nitidulous, beneath opaque, minutely and rather sparsely pilosulose; petioles 0.3–0.5 cm. long, very minutely pilosulose; inflorescence terminal, 1-flowered; peduncle 0.3–0.4 cm. long, essentially glabrous; pedicel 0.2–0.3 cm. long, very minutely pilosulose; calyx-lobes linear-trigonal, obtusish, about 0.25 cm. long, minutely pilosulose, eglandular within; corolla, anthers, and ovary unknown; follicles terete, relatively stout, 5–7 cm. long, essentially glabrous without; seeds 0.5–0.6 cm. long, the pale tawny coma about 1.8 cm. long.

CUBA: ORIENTE: prope Maravi, in pinetis, *Ekman 4051* (B, TYPE).

I have not been able to examine the type specimen, hence the preceding description is merely an adaptation of Urban's.

## XI. GALACTOPHORA Woodson

**Galactophora** Woodson, Ann. Mo. Bot. Gard. 19: 49. 1932.

Lactescent, suffruticose undershrubs or suffrutescent herbs. Branches erect or ascending, opposite to occasionally alternate above. Leaves opposite, coriaceous to subcoriaceous, petiolate to subsessile, entire, penninerved, eglandular; petioles somewhat girdling at the node into an obscurely appendiculate, stipular ring. Inflorescence terminal to subterminal, scorpioidally corymbose to subumbellate, bracteate, relatively few-flowered. Calyx 5-parted, the lobes equal to subequal, cleft nearly to the receptacle, imbricated, foliaceous, bearing within several to many indefinitely distributed squamellae. Corolla infundibuliform, large and showy, the proper-tube straight, inappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia with a conspicuous protuberant base borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the 5-gonal, fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, coalescent, and usually somewhat adnate to the ovary. Follicles 2, apocarpous, terete, acuminate, dehiscent along the ventral suture, containing many dry, truncate, apically comose seeds.

Type species: *Galactophora crassifolia* (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 50. 1932.

### KEY TO THE SPECIES

- a. Inflorescence 5-10-flowered, corymbose; calyx-lobes linear-lanceolate....  
.....1. *G. pulchella*
- aa. Inflorescence 1-5-flowered, subumbellate; calyx-lobes broadly ovate to ovate-lanceolate.
  - b. Calyx and corolla puberulent, bearing irregularly interspersed, glandular aculei.

- c. Calyx-lobes 1.5–2.0 cm. long; leaves broadly oblong to oblong-lanceolate.....2. *G. crassifolia*
- cc. Calyx-lobes 0.5–0.6 cm. long; leaves ovate.....3. *G. Schomburgkiana*
- bb. Calyx and corolla glabrous.
  - c. Corolla-tube 3–4 cm. long, the lobes about 1.5 cm. long; leaves broadly oblong.....4. *G. calycina*
  - cc. Corolla-tube 5.0–5.5 cm. long, the lobes about 4.5 cm. long; leaves broadly ovate.....5. *G. magnifica*

1. *Galactophora pulchella* Woodson, Ann. Mo. Bot. Gard. 19: 51. 1932.

Stems relatively stout, softly puberulent when young, soon becoming glabrate; leaves opposite, subsessile and somewhat amplexicaul, broadly ovate, apex obtusish, base abruptly rounded and obscurely cordate, 3.5–7.0 cm. long, 2.5–4.5 cm. broad, glabrous, or either surface softly puberulent when young; petioles 0.1–0.2 cm. long; inflorescence corymbose, 5–10-flowered; peduncle 3–5 cm. long, softly puberulent; pedicels 1.0–1.5 cm. long, softly puberulent with small, glandular aculei interspersed rather irregularly; bracts inconspicuous; calyx-lobes linear-lanceolate, 0.5–0.75 cm. long, minutely puberulent with interspersed aculei; corolla infundibuliform essentially glabrous without, or with extremely inconspicuous indument and aculei, the proper-tube 0.5–0.6 cm. long, about 0.2 cm. in diameter at the base, the throat 1.5 cm. long, about 0.4 cm. in diameter at the orifice, the lobes obliquely oblong-obovate, obtuse, 1.0–1.25 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers lanceolate-sagittate, 0.5–0.6 cm. long, glabrous; ovary oblong-ovoid, about 0.15 cm. long, glabrous; stigma about 0.15 cm. long; nectaries somewhat shorter than the ovary; follicles unknown.

BRAZIL: AMAZONAS [?]: Cano Pimicheiro, June, 1854, *Spruce 3718* (K, TYPE, MBG, photograph and analytical drawings).

2. *Galactophora crassifolia* (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 50. 1932.

*Amblyanthera crassifolia* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 143. 1860.

*Echites crassifolia* Spruce, ex Muell.-Arg. loc. cit. 1860, nom. nud. in synonym.



*Rhodocalyx crassifolius* (Muell.-Arg.) Miers, Apoc. So. Am. 139. 1878.

*Mandevilla crassifolia* Muell.-Arg. ex K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895, sphalm.

*Mandevilla crassifolia* (Spruce) K. Sch. ex Mgf. in Fedde, Rep. Spec. Nov. 20: 24. 1924, sphalm.

Stems relatively stout, minutely puberulent with interspersed, glandular aculei when young, becoming glabrate; leaves opposite, subsessile, broadly oblong to oblong-lanceolate, apex obtuse to rounded, base rather abruptly rounded and obscurely cordate, more or less amplexicaul, 5–12 cm. long, 3–5 cm. broad, coriaceous, glabrous; petioles 0.1–0.2 cm. long, glabrous to aculeate as upon the stem; inflorescence subumbellate, 1–5-flowered; pedicels 1.2–1.5 cm. long, glabrous to minutely puberulent; bracts scarious, about 0.1 cm. long; calyxlobes ovate, acute, 1.5–2.0 cm. long, more or less conspicuously aculeate; corolla infundibuliform, conspicuously aculeolate without, the proper-tube 2.5–3.0 cm. long, about 0.2 cm. in diameter at the base, the throat 3 cm. long, about 2 cm. in diameter at the orifice, the lobes obliquely obovate, obtuse, 2.5–3.0 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers lanceolate-sagittate, 0.6–0.7 cm. long, glabrous, or infrequently sparsely barbellate at the base of the narrow auricles; ovary oblong-ovoid, about 0.3 cm. long, glabrous; stigma 0.15 cm. long; nectaries about half equalling the ovary; follicles relatively stout, rigid, 12–16 cm. long, glabrous; seeds 0.3 cm. long, the tawny coma about 2 cm. long.

VENEZUELA: AMAZONAS: Cerro Yapacana, upper Rio Orinoco, alt. 100 m., April, 1931, *Holt & Blake 716* (US).

BRITISH GUIANA: exact locality lacking, Dec., 1842, *Schomburgk 1551* (B).

BRAZIL: AMAZONAS: prope San Carlos, ad Rio Negro, 1853–4, *Spruce 3136* (B, Camb., K, V, MBG, photograph and analytical drawings); in campis arenosis prope Faro, date lacking, *Ducke 8434* (B); Manãos, July 31, 1900, *Ule 5175* (B); MATTO GROSSO: Juruena Procedencia, April, 1909, *Hoehne 1804* (B); Cataqui-Imain, Jan., 1919, *Kuhlmann 2252* (B).

**3. *Galactophora Schomburgkiana* Woodson, Ann. Mo. Bot. Gard. 19: 50. 1932.**

Stems relatively stout, softly puberulent when young, soon

becoming glabrate; leaves opposite, subsessile, broadly ovate, apex obtusish, base abruptly rounded, obscurely cordate and more or less amplexicaul, 4–7 cm. long, 2.5–4.5 cm. broad, coriaceous, softly puberulent when young, soon becoming glabrate; petioles 0.1–0.2 cm. long; inflorescence subumbellate, 3–5-flowered; pedicels 1.0–1.5 cm. long, softly puberulent with interspersed aculei; bracts extremely inconspicuous; calyx-lobes ovate, acutish, 0.5–0.6 cm. long, minutely puberulent, evidently rarely aculeolate; corolla infundibuliform, aculeate-striate without, the proper-tube 2–3 cm. long, about 0.2 cm. in diameter at the base, the throat 3.0–3.5 cm. long, about 0.8 cm. in diameter at the orifice, the lobes obliquely obovate, obtuse, 1.0–1.2 cm. long; stamens inserted at the base of the corolla-throat, the anthers and gynoecium unseen; follicles relatively stout, 14 cm. long, densely aculeolate; seeds 0.6 cm. long, the tawny coma 1.5–2.0 cm. long.

BRITISH GUIANA: exact locality and date lacking, *Schomburgk s. n.* (K, TYPE, MBG, photograph and analytical drawings).

4. *Galactophora calycina* (Hub.) Woodson, Ann. Mo. Bot. Gard. 19: 50. 1932.

*Dipladenia calycina* Hub. ex Ducke, Archiv. Jard. Bot. Rio Janeiro 3: 247. 1922; Bol. Mus. Goeldi 7: 113. 1913, nom. nud.

### Plate 2.

Stems relatively stout, glabrous; leaves opposite, subsessile, broadly oblong, apex obtuse or rounded, frequently somewhat retuse, base rather abruptly rounded, obscurely cordate and more or less amplexicaul, 3–6 cm. long, 2–4 cm. broad, coriaceous, glabrous; petioles about 0.1 cm. long; inflorescence subumbellate, 1–5-flowered; pedicels 0.5–0.7 cm. long, glabrous; bracts very inconspicuous; calyx-lobes ovate, acute, 1.5–2.0 cm. long, glabrous; corolla infundibuliform, glabrous without, the proper-tube 1.5–2.0 cm. long, about 0.2 cm. in diameter at the base, the throat 1.5–2.0 cm. long, about 1 cm. in diameter at the orifice, the lobes broadly obovate, obtuse, 1.2–1.6 cm. long,

widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly sagittate, 0.6–0.7 cm. long, glabrous; ovary ovoid, about 0.4 cm. long, glabrous; stigma 0.2 cm. long; nectaries somewhat less than half equalling the ovary; follicles unknown.

BRAZIL: PARA: Faro, inter fruticulos loco Campos do Tigre, Dec. 31, 1919, *Ducke 11393* (B, S. MBG, photograph and analytical drawings); Cachoeira, sandy ground of new clearing, 1898, *Gwynne-Vaughan 33* (K, MBG, photograph and analytical drawings).

5. *Galactophora magnifica* Woodson, *Ann. Mo. Bot. Gard.* 19: 382. 1932.

Stems relatively stout, glabrous; leaves opposite, sessile, broadly ovate, apex obtuse, base broadly cordate and amplexicaul, 4.5–5.0 cm. long, 3.0–3.5 cm. broad, coriaceous, wholly glabrous; inflorescence subumbellate, few- (in our specimen 3-) flowered; pedicels 0.9–1.0 cm. long, glabrous; bracts extremely minute, scarious; calyx-lobes broadly ovate-lanceolate, acuminate, 2.0–2.5 cm. long, glabrous; corolla glabrous without, the proper-tube 2.0–2.3 cm. long, about 0.4 cm. in diameter at the base, the throat broadly campanulate, 2.8–3.0 cm. long, about 2.5 cm. in diameter, the lobes obliquely ovate, shortly acuminate, 4.5 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly sagittate, 0.8 cm. long, glabrous; ovary oblongoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries somewhat shorter than the ovary; follicles unknown.

BRAZIL: MATTO GROSSO: Procedencia Juruena, campo humido e pantuoso, April, 1909, *Hoehne 1759* (US, TYPE, MBG, photograph and analytical drawings).

## XII. SALPINCTES Woodson

*Salpinctes* Woodson, in Gleason, *Bull. Torrey Bot. Club* 58: 453. 1931.

Lactescent, suffrutescent herbs or suffruticose undershrubs. Stems erect to ascending, terete. Leaves opposite to subverticillate, shortly petiolate to essentially sessile, penninerved, eglandular. Inflorescence terminal, uniflorous in our

specimens. Calyx 5-parted, the lobes equal to subequal, cleft nearly to the receptacle, imbricated, bearing many indefinitely distributed squamellae within. Corolla salverform, the tube straight, exappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular. Carpels 2, united at the apex by an elongate, common style surmounted by the pentagonal-fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 2, separate. Follicles apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, truncate, apically comose seeds.

Type species: *Salpinctes kalmiaefolius* Woodson, in Gleason, Bull. Torrey Bot. Club 58: 453. 1931.

#### KEY TO THE SPECIES

- a. Leaves oblong-ovate, 0.8–1.0 cm. broad, strictly opposite; stems glabrous .....1. *S. kalmiaefolius*
- aa. Leaves oblong-linear, 0.2–0.4 cm. broad, opposite to subverticillate; stems scabrous-bullate.....2. *S.*

1. *Salpinctes kalmiaefolius* Woodson, in Gleason, Bull. Torrey Bot. Club 58: 453. *pl.* 37. 1931.

#### *Plate 3.*

Stems relatively stout, 2–5 dm. tall (fide Tate), wholly glabrous; leaves opposite, subsessile, oblong-ovate, apex obtuse to rounded, base rounded to subtruncate, 2–4 cm. long, 0.8–1.0 cm. broad, heavily coriaceous, the margin strongly revolute in desiccation, wholly glabrous, lustrous above, opaque beneath; petioles 0.1–0.15 cm. long; inflorescence terminal, bearing a solitary, showy, bright pink flower; peduncle essentially obsolete; pedicels 0.15–0.2 cm. long, glabrous; bracts broadly triangular-ovate, about 0.1 cm. long, scarious, caducous; calyxlobes ovate-lanceolate, acuminate, 0.45–0.5 cm. long, scarious, glabrous; corolla salverform, glabrous without, the tube 2.5–3.5

cm. long, about 0.125 cm. in diameter at the base, slightly dilating toward the orifice, the lobes obliquely obovate, obtuse, 2.5–3.0 cm. long, widely spreading; stamens inserted somewhat below midway within the corolla-tube, the anthers narrowly sagittate, 0.45 cm. long, glabrous; ovary ovoid, about 0.125 cm. long, glabrous; stigma 0.15 cm. long; nectaries 2, somewhat shorter than the ovary; follicles unknown.

BRITISH GUIANA: dryish slopes of Savanna Hills, alt. 4400 ft., Aug., 1928–April, 1929, *Tate 836* (NY, TYPE, MBG, photograph and analytical drawings).

2. *Salpinctes* (?) *duidae* Woodson, in Gleason, Bull. Torrey Bot. Club 58: 454. 1931.

Stems relatively stout, 1.5–3.0 dm. tall, scabrous-bullate; leaves crowded, opposite to subverticillate, essentially sessile, oblong-linear, 3–6 cm. long, 0.2–0.4 cm. broad, heavily coriaceous, the margins strongly revolute, glabrous and lustrous above, opaque and slightly scabridulous to glabrate beneath; inflorescence evidently uniflorous, but the flowers unknown at present; follicles relatively stout, essentially continuous, 10–12 cm. long, glabrous; seeds unknown.

BRITISH GUIANA: dry ridge tops, Savanna Hills, alt. 4400 ft., Aug., 1928–April, 1929, *Tate 805* (NY, TYPE, MBG, photograph).

This genus is no better understood than when first published, due to the lack of additional specimens or other data concerning it. At the time of original publication the genus *Dipladenia* A. DC. was considered to be distinct from *Mandevilla* Lindl. upon the basis of the geminate nectaries of the former. Since the discovery of manifest intergradation between these genera and their subsequent consolidation, the status of *Salpinctes*, also based in part upon geminate nectaries, has been somewhat uneasy. The situation of *Salpinctes* is not exactly parallel, however, because of its relatively few species, also characteristic of its immediate relatives. Hence, the probability of intergradation is somewhat less imminent than amongst the numerous and wide-ranging species of *Mandevilla* and *Dipladenia*. Should a *Galactophora* be found with salverform corollas, and a *Salpinctes* with five concrescent nectaries, however,

the existing criteria separating those genera would become too attenuated for practicality.

### XIII. PELTASTES Woodson

**Peltastes** Woodson, Ann. Mo. Bot. Gard. 19: 375. 1932.

Lactescent, fruticose or suffruticose lianas. Branches opposite, or the uppermost alternate. Leaves opposite, petiolate, peltate, entire, penninerved, eglandular, firmly membranaceous to subcoriaceous; petioles somewhat girdling at the node into an obscurely appendiculate, stipular ring. Inflorescence lateral, opposite, infrequently terminal or subterminal, aggregate-dichasial, bracteate, few- to several-flowered. Calyx 5-parted, the lobes subequal to more or less conspicuously dissimilar, cleft nearly to the receptacle, imbricated, strikingly foliaceous, bearing within at the base many indefinitely distributed squamellae. Corolla infundibuliform, large and showy, the proper-tube straight, exappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute; stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia with a conspicuous protuberant base borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular. Carpels 2, united at the apex by a slender stylar shaft surmounted by the capitate-fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, essentially separate. Follcles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, rostrate, apically comose seeds.

Type species: *Peltastes peltatus* (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932.

#### KEY TO THE SPECIES

a. Anthers glabrous.

- b. Calyx-lobes 1.0–1.5 cm. long; corolla-lobes broadly and obliquely obovate, obtuse, 2.5–3.0 cm. long; plants of southeastern Brazil. .1. *P. malvaeflorus*
- bb. Calyx-lobes 1.5–2.0 cm. long; corolla-lobes dolabriform, acute to acuminate, 2.0–2.5 cm. long; plants of Paraguay. . . . . 2. *P. stemmadeniiflorus*

aa. Anthers pubescent dorsally.

- b. Corolla-throat broadly conical to campanulate, at least above.
- c. Corolla 4.0–5.5 cm. long; species of South America.
- d. Calyx-lobes obovate to broadly obovate-oblong; corolla proper-tube 2.2–2.5 cm. long; plants of Colombia and Venezuela...3. *P. colombianus*
- dd. Calyx-lobes narrowly oblong to oblong-elliptic; corolla proper-tube 0.9–1.0 cm. long; plants of southeastern Brazil.....4. *P. peltatus*
- ec. Corolla 7.8–8.3 cm. long; plants of Panama and Costa Rica...5. *P. isthmicus*
- bb. Corolla-throat narrowly conical to subtubular-conical; plants of Bolivia .....6. *P. giganteus*

1. ***Peltastes malvaeflorus*** Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932.

*Plate 4.*

Stems relatively stout, densely ferruginous-lanulose when young, eventually becoming glabrate; leaves opposite, broadly ovate, rather shortly acuminate at the apex, base broadly rounded, 10–16 cm. long, 7–11 cm. broad, firmly membranaceous, above minutely and rather sparsely ferruginous-puberulent when young, eventually becoming glabrate, beneath minutely and persistently ferruginous-puberulent; petioles 2–4 cm. long, densely and persistently ferruginous-lanulose; inflorescences lateral, opposite, 3–5-flowered, the peduncle about equalling the length of the subtending petioles, densely ferruginous-lanulose; pedicels 2.3–2.5 cm. long, ferruginous-lanulose; bracts foliaceous, obovate to obovate-lanceolate, 0.5–2.0 cm. long; calyx-lobes oblong to oblong-lanceolate, acute to obtuse, 1.0–1.5 cm. long, minutely and rather inconspicuously ferruginous-puberulent without; corolla infundibuliform, glabrous without, the proper-tube 1.0–1.2 cm. long, about 0.6 cm. in diameter at the base, the throat broadly conical-campanulate, dilating almost directly above the insertion of the stamens, 2.0–2.3 cm. long, 2.3–2.5 cm. in diameter at the orifice, the lobes broadly and obliquely obovate, obtuse, 2.5–3.0 cm. long, slightly spreading; anthers 1.1–1.3 cm. long, glabrous; ovary about 0.2 cm. long, essentially glabrous; nectaries fleshy, essentially equal, about equalling the ovary; stigma 0.3 cm. long; follicles relatively stout, 20–25 cm. long, the tips more or less persistently connate, glabrous or very minutely papillate; seeds 2.3 cm. long, the pale orange coma about 5 cm. long.

BRAZIL: PARANA: Valhinos ad marginem silvae primaevae, Nov. 11, 1910, *Dusen* 10851 (G, MBG, TYPE, S, US); Roca Nova, ad marginem silvae, March 15, 1909, *Dusen*, 7884 (S); Ponta Grossa, in silvula, Jan. 15, 1909, *Dusen* 7552 (NY, S); RIO GRANDE DO SUL: Silveira Martina, prope Santa Maria, in silva primaeva, March 6, 1893, *Malme* 690 (S, COTYPE, MBG, photograph); prope São Leopoldo, Febr., year lacking, *Dutra* 301 (S).

2. *Peltastes stemmadeniiflorus* Woodson, Ann. Mo. Bot. Gard. 19: 377. 1932.

Stems relatively stout, densely ferruginous-lanulose when young, eventually becoming glabrate; leaves opposite, broadly ovate, apex very shortly acute to acuminate, base broadly rounded, 10–30 cm. long, 7–15 cm. broad, minutely and rather sparsely ferruginous-puberulent when young, eventually becoming glabrate upon both surfaces; petioles 3–7 cm. long, minutely ferruginous-lanulose when young, eventually becoming glabrate; inflorescences lateral, opposite, 8–10-flowered, the peduncle somewhat shorter than the subtending petioles, minutely ferruginous-hirtellous; pedicels 1.0–1.5 cm. long, minutely ferruginous-hirtellous; bracts foliaceous, obovate-lanceolate, 0.4–1.2 cm. long; calyx-lobes oblong- to elliptic-lanceolate, acute to acuminate, 1.5–2.0 cm. long, minutely ferruginous-puberulent without; corolla infundibuliform, glabrous without, the proper-tube 1.3–1.4 cm. long, about 0.4 cm. in diameter at the base, the throat broadly conical to campanulate, dilating almost directly above the insertion of the stamens, 3.0–3.2 cm. long, 1.2–1.3 cm. in diameter at the orifice, the lobes broadly dolabriform, acute to acuminate, 2.0–2.5 cm. long, slightly spreading; anthers 1.2–1.3 cm. long, glabrous; ovary about 0.25 cm. long, essentially glabrous; nectaries fleshy, essentially equal, about equalling the ovary; stigma 0.25 cm. long; follicles unknown.

PARAGUAY: in altaplanitie et declivibus, Sierra de Amambay, Dec., 1907, *Rojas* 9838 (V, TYPE, MBG, photograph and analytical drawings); in woods, Mbuvena, Febr., 1931, *Jørgensen* 4711 (MBG, NY); in reg. fluminis Alto Parana, 1909–10, *Fiebrig* 5841 (G, US).

The distinction of *P. malvaeflorus* and *P. stemmadeniiflorus* may well be questioned. The plants are of much the same general aspect, although it is believed that the rather slight di-



mensional differences are significant. The corolla-lobes also appear to invite specific segregation. The corolla-throat of the latter species is much narrower than that of the former; and such differences, when taken into consideration with the supposedly distinct, if adjacent, ranges of the species have prompted their separate maintenance, at least until more ample, contradictory evidence is forthcoming.

**3. *Peltastes colombianus* Woodson, Ann. Mo. Bot. Gard. 19: 378. 1932.**

Stems relatively stout, densely ferruginous-lanulose when young, eventually becoming glabrate; leaves opposite, broadly ovate, very shortly subcaudate-acuminate, base broadly rounded to subtruncate, 16–28 cm. long, 10–22 cm. broad, above very minutely puberulent when young, soon becoming glabrate, beneath persistently puberulent-papillate; petioles 5–11 cm. long, minutely ferruginous-puberulent to glabrate; inflorescences 7–15-flowered, the peduncle densely and persistently ferruginous-lanulose; pedicels 1.5–2.0 cm. long, minutely ferruginous-lanulose; bracts foliaceous, obovate to obovate-oblong, 1.0–1.6 cm. long; calyx-lobes obovate to obovate-elliptic, acute to obtuse, 2.3–3.0 cm. long, obtuse to very shortly acuminate, very minutely and inconspicuously puberulent without; corolla infundibuliform, glabrous without, the proper-tube 2.2–2.5 cm. long, about 0.4 cm. in diameter at the base, the throat not directly dilated above the insertion of the stamens, differentiated into a more or less distinct upper- and lower-throat, the former 1.0–1.3 cm. long, scarcely broader than the proper-tube, the latter abruptly dilated, campanulate, 0.8–1.0 cm. long, about 1.2–1.5 cm. in diameter at the orifice, the lobes obliquely obovate-dolabriform, obtuse, 1.2–1.4 cm. long, widely spreading to somewhat reflexed; anthers 1.2–1.3 cm. long, minutely hirtellous dorsally; ovary about 0.2 cm. long, minutely ferruginous-tomentulose; nectaries essentially equal, fleshy, about equalling the ovary; follicles unknown.

COLOMBIA: MAGDALENA: forest near a stream, alt. 2000 ft., vicinity of Santa Marta, June 27, 1899, *Smith 2412* (G, MBG, TYPE, NY, US).

VENEZUELA: CARABOBO: Guaremales, road from Puerto Cabello to San Felipe, in forest, alt. 350 m., July 2, 1920, *Pittier 8920* (G, NY, US).

Mr. Smith describes his plant as a vine 25 feet tall, with "corolla green, lobes pale yellowish green."

**4. *Peltastes peltatus*** (Vell.) Woodson, *Ann. Mo. Bot. Gard.* 19: 376. 1932.

*Echites peltata* Vell. *Fl. Flum.* 110. 1830; *Icon.* 3: *pl.* 32. 1827; A. DC. in DC. *Prodr.* 8: 465. 1844; Muell.-Arg. in Mart. *Fl. Bras.* 6<sup>1</sup>: 159. *pl.* 53, *fig.* 2. 1860.

*Echites plicata* A. DC. loc. cit. 454. 1844.

*Echites macrocalyx* Muell.-Arg. loc. cit. 160. 1860.

*Stipecoma peltata* (Vell.) Miers, *Apoc. So. Am.* 134. 1878.

*Stipecoma plicata* (A. DC.) Miers, loc. cit. 1878.

*Stipecoma pulchra* Miers, loc. cit. 135. *pl.* 18. 1878.

*Stipecoma mucronata* Miers, loc. cit. 1878.

*Stipecoma macrocalyx* (Muell.-Arg.) Miers, loc. cit. 136. 1878.

*Stipecoma speciosa* Miers, loc. cit. 1878.

*Stipecoma ovata* Miers, loc. cit. 137. *pl.* 19. 1878.

*Stipecoma parabolica* Miers, loc. cit. 1878.

*Peltastes macrocalyx* (Muell.-Arg.) Woodson, loc. cit. 1932.

Stems relatively stout, densely ferruginous-lanulose when young, becoming glabrate; leaves opposite, broadly ovate to obovate-oval, apex very shortly acuminate to essentially rounded, base broadly rounded to subtruncate, 5–30 cm. long, 2.5–18 cm. broad, firmly membranaceous, above glabrous, or very indefinitely papillate when young, beneath minutely and persistently ferruginous-lanulose; petioles 1.8–10.0 cm. long, minutely and persistently ferruginous-lanulose; inflorescence 5–20 flowered, the peduncle densely ferruginous-lanulose, about equalling the subtending petioles; pedicels 1.0–1.3 cm. long, minutely ferruginous-lanulose; bracts oblong-spathulate, foliaceous, 0.7–1.5 cm. long; calyx-lobes narrowly oblong to oblong-elliptic, acute to acuminate, 1.5–1.7 cm. long, minutely and rather sparsely ferruginous-puberulent without; corolla

infundibuliform, glabrous without, the proper-tube 0.9–1.0 cm. long, about 0.4–0.45 cm. in diameter at the base, the throat not directly dilated above the insertion of the stamens, differentiated into a more or less distinct upper- and lower-throat, the former 0.6–0.7 cm. long, scarcely broader than the proper-tube, the latter abruptly dilated, broadly campanulate, 0.8–0.9 cm. long, about 1.2–1.3 cm. in diameter at the orifice, the lobes obliquely dolabriform, shortly acuminate, 1.6–1.7 cm. long, somewhat spreading; anthers 1.1–1.2 cm. long, minutely hirtellous dorsally; ovary about 0.2 cm. long, finely ferruginous-puberulent to essentially glabrate; nectaries fleshy, essentially equal, about equalling the ovary; stigma 0.2 cm. long; follicles stout, falcate, usually persistently united at the tips, 15–25 cm. long, glabrous, or essentially so; seeds 2.0–2.5 cm. long, the pale tawny coma 5.0–5.5 cm. long.

BRAZIL: MINAS GERAES: Ilheos, 1859–60, *Wawra & Maly 241* (V); Serra de Caldas, Oct. 25, 1873, *Mosen 622* (C, S); Caldas, prope Rio de Machada, Nov., 1854 *Lindberg 191* (S); Caldas, Febr. 24, 1862, *Regnell III 883* (C, S, US); Lagôa Santa, date lacking *Warming s.n.* (C, NY); RIO DE JANEIRO: Serra d'Estrella, Nov. 15, 1874, *Glaziov 7763* (US); data incomplete, *Schott 5398* (V); *Widgren s.n.* (S); SÃO PAULO: Jaragua, "Buschwald," Dec. 22, 1912, *Brade 5688* (S); prope Rio Grande inter Santos et urbem S. Paulo, 1902, *Wacket s.n.* (C); DATA INCOMPLETE: *Mikan s.n.* (V); *Biedel s.n.* (G, V); *Glaziov 4879* (C); *Glaziov 11188* (C).

As specimens of *Peltastes* from southern Brazil have accumulated for study, the validity of *P. macrocalyx* has appeared more and more dubious. The pubescence of the ovary evidently does not distinguish it, as believed by Mueller, since the majority of specimens, doubtless of *P. peltatus* as shown by other characters, demonstrates to a greater or less degree much the same type of indument. Glabrate individuals are rare. Hence, it appears desirable to consolidate the two species, at least until such time when additional criteria will have been discovered. Miers' numerous species are all certainly insignificant variations of the frequent and widespread *P. peltatus* prompted largely by fluctuations of leaf size as well as by the relative abundance or sparsity of vegetative indument, largely reflecting the relative age of the portion of the plants selected as specimens.

**5. *Peltastes isthmicus* Woodson, spec. nov.**

Fruticosa volubilis; ramulis teretibus crassiusculis juventate dense ferrugineo-lanulosis tandem glabratiss; foliis oppositis longe petiolatis peltatis late ovatis apice abruptissime brevissimeque acuminatis basi late rotundatis 10–30 cm. longis 8–20 cm. latis firmiter membranaceis supra juventate sparse inconspicueque puberulo-papillatis mox glabratiss subtus juventate dense ferrugineo-lanulosis tandem glabratiss; petiolis 5–12 cm. longis ut in ramulo vestitis; inflorescentiis 10–15-floris pedunculo petiolis subaequante minute denseque ferrugineo-lanuloso; pedicellis 1.8–2.0 cm. longis ut in pedunculo vestitis; bracteis foliaceis oblongo-spathulatis 0.8–1.7 cm. longis; calycis laciniis oblongo-obovatis breviter subcaudato-acuminatis 2.8–3.0 cm. longis basi inconspicue puberulo-papillatis; corolla infundibuliformi extus glabra tubo proprio 2.3–2.5 cm. longo basi ca. 0.5 cm. diametro metiente faucibus basi prope insertionem staminum vix inflatis deinde late campanulatis 2.0–2.3 cm. longis ostio ca. 1.9–2.0 cm. diametro metiente lobis oblique obovatis haud acuminatis 3.5 cm. longis patulis; antheris 1.2 cm. longis dorso hirtellis; ovario ca. 0.18 cm. longo glabro; nectariis carnosiss ovario subaequantibus; stigmate 0.2 cm. longo; folliculis crassis falcatis 22–25 cm. longis irregulariter ferrugineo-papillatis; seminibus haud visis.

Stems relatively stout, densely ferruginous-lanulose when young, becoming glabrate; leaves opposite, long-petiolate, peltate, broadly ovate, apex very abruptly and shortly acuminate, base broadly rounded, 10–30 cm. long, 8–20 cm. broad, firmly membranaceous, above sparsely and inconspicuously puberulent-papillate in youth, soon becoming glabrate, beneath densely ferruginous-lanulose when young, becoming glabrate; petioles 5–12 cm. long, indument as upon the stem; inflorescence 10–15-flowered, the peduncle about equalling the subtending petioles, minutely and densely ferruginous-lanulose; pedicels 1.8–2.0 cm. long, clothed as upon the peduncle; bracts foliaceous, oblong-spathulate, 0.8–1.7 cm. long; calyx-lobes oblong-ovate, shortly subcaudate-acuminate, 2.8–3.0 cm. long, inconspicuously puberulent-papillate at the base without;

corolla infundibuliform, glabrous without, the proper-tube 2.3–2.5 cm. long, about 0.5 cm. in diameter at the base, the throat broadly campanulate, 2.0–2.3 cm. long, about 1.9–2.0 cm. in diameter at the orifice, the lobes obliquely obovate, not acuminate, about 3.5 cm. long, spreading; anthers 1.2 cm. long, hirtellous dorsally; ovary about 0.18 cm. long, glabrous; nectaries fleshy, about equalling the ovary; stigma 0.2 cm. long; follicles stout, falcate, 22–25 cm. long, irregularly ferruginous-papillate; seeds not seen.

PANAMA: CHIRIQUI: vicinity of San Felix, alt. 0–120 m., Dec., 1911, *Pittier 5125* (US, TYPE, MBG, photograph).

COSTA RICA: GUANACASTE: Nicoya, 1900, *Tondus s.n.* (US).

The affinities of this species, notable as the sole Central American representative of a South American genus, are set forth in the key to species. The specimen collected by Tondus upon the Nicoya Peninsula of Costa Rica is relegated to this species merely upon presumption, as it is completely sterile.

6. *Peltastes giganteus* Woodson, Ann. Mo. Bot. Gard. 19: 378. 1932.

Stems relatively stout, densely ferruginous-lanulose when young, eventually becoming glabrate; leaves opposite, broadly ovate, apex very shortly and abruptly acuminate to obtuse, base broadly rounded, 18–35 cm. long, 9–20 cm. broad, firmly membranaceous to subcoriaceous, above minutely ferruginous-lanulose when very young, soon becoming glabrate, beneath persistently ferruginous-lanulose; petioles 7–12 cm. long, minutely ferruginous-lanulose when young, becoming glabrate; inflorescence 4–5-flowered, the peduncle somewhat shorter than the subtending petioles, minutely and densely ferruginous-lanulose; pedicels 1 cm. long, ferruginous-lanulose; bracts foliaceous, oblong-lanceolate, shortly acuminate, 0.8–2.0 cm. long; calyx-lobes obovate-oblong, obtuse, 0.8–1.5 cm. long, minutely puberulent-papillate toward the base, otherwise glabrous; corolla infundibuliform, glabrous without, the proper-tube 1.7–1.8 cm. long, about 0.35 cm. in diameter at the base, the throat narrowly conical or subtubular-conical, dilating almost directly above the insertion of the stamens, 1.8–2.0 cm. long, 0.8–

0.9 cm. in diameter at the orifice, the lobes obovate-dolabriform, acute, 1.0–1.3 cm. long, somewhat spreading; anthers 1.2 cm. long, lanulose dorsally; ovary about 0.25 cm. long, minutely lanulose; nectaries only slightly fleshy, irregularly cleft, about equalling the ovary; stigma 0.2 cm. long; follicles unknown.

BOLIVIA: data incomplete, *Bang* 2804 (MBG, TYPE, NY, US); *Bang* 2404 (C, US).

The tubular corolla-throat sets this species well apart from its congeners, as does the irregularly cleft nectary.

#### XIV. STIPECOMA Muell.-Arg.

**Stipecoma** Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860; Miers, Apoc. So. Am. 132. 1878, in part; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 166. 1895.

Glabrous, suffruticose lianas. Stems volubile, terete; branches usually opposite below (?), becoming alternate above. Leaves opposite, petiolate, the blade peltate, penninerved, eglandular, entire or slightly sinuous, rigidly chartaceous or subcoriaceous; petioles very obscurely girdling at the node. Inflorescence a lateral, alternate, bostrychoid raceme. Flowers pedicellate, subtended by 1–3 scarious bracts. Calyx 5-parted, the lobes equal or subequal, cleft nearly to the receptacle, scarious, bearing few to several internal, glandular squamellae in groups alternate with the lobes. Corolla salverform, the tube cylindrical, somewhat dilated at the insertion of the stamens, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, epipetalous, the anthers coherent, consisting of 2 longitudinal, apically convergent, bilocular sporangia borne ventrally near the apex of an enlarged, sagittate, acutely biauriculate, dorsally pilose connective, the filament subcylindrical, pilose, the pollen granular. Carpels 2, subinferior, apocarpous, united at the apex by an elongate, stylar shaft surmounted by the fusiform stigma; ovules many, borne upon an axile, binate placenta. Nectaries 5, conerescent or essentially so. Follicles 2, apocarpous, terete, continuous, dehiscing along the ventral suture, containing many dry, rostrate, apically comose seeds; embryo straight, typically dicotyledonous.

Type species: *Stipecoma peltigera* (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 176. 1860.

1. *Stipecoma peltigera* (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 176. *pl.* 53, *fig.* 1. 1860; Miers, Apoc. So. Am. 133. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 166. 1895.

*Echites peltigera* Stadelm. Flora 24<sup>1</sup>: Beibl. 21. 1841; A. DC. in DC. Prodr. 8: 447. 1844.

*Echites tropaeolifolia* A. DC. loc. cit. 1844.

Glabrous, suffruticose lianas; stems terete, relatively slender; leaves opposite, petiolate, the blade peltate, rigidly chartaceous to subcoriaceous, ovate, apex acuminate, base rather broadly rounded, 4–6 cm. long, 3.0–4.5 cm. broad, the petiole 2.5–3.0 cm. long; inflorescence usually somewhat surpassing the length of the subtending leaves, bearing 5–14 “obscurely rose-colored” flowers; pedicels 0.75 cm. long, somewhat accrescent in fruit, the subtending bracts scarious, minute; calyxlobes ovate, broadly acute, about 0.2 cm. long, scarious; corolla salverform, the tube cylindrical, about 1.5 cm. long, somewhat dilated at the insertion of the stamens, the lobes obliquely obovate, acuminate, about equalling the length of the tube, widely spreading; stamens inserted about midway within the corolla-tube, the anthers rather narrowly sagittate, pilose dorsally toward the tip; ovary oblongoid, glabrous, rather gradually produced into the style; stigma fusiform; nectaries crescent, variously lobed and cleft, nearly equalling the ovary; follicles as in the generic description.

BRAZIL: GOYAZ: ad Serra d’Ourada, date lacking, *Pohl 159?* (V, COTYPE, MBG, photograph).

The description and dimensions of the flowers and reproductive organs have been taken from the original account by Mueller, since the one specimen available for my study is sterile. Mueller cited this species from the provinces of Bahia (*Martius s.n.*) and Minas Geraes (*St. Hilaire s.n.*), as well as listing additional collections in Goyaz by Weddell (*s.n.*) and Riedel (932). These specimens have not been available for study, and

the species, apparently rare in the field, has not been represented in recent collections available for examination.

*Stipecoma* simulates *Peltastes* in its peltate leaves, but differs in its salverform corolla, scarious calyx-lobes with relatively few, alternate squamellae, and more narrowly rostrate seeds.

#### EXCLUDED SPECIES

The following are apparently all referable to *Peltastes peltatus* (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932 (*Echites peltata* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 32. 1827):

*Stipecoma macrocalyx* (Muell.-Arg.) Miers, Apoc. So. Am. 136. 1878 (*Echites macrocalyx* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 160. 1860).

*Stipecoma mucronata* Miers, Apoc. So. Am. 135. 1878.

*Stipecoma ovata* Miers, Apoc. So. Am. 137. pl. 19. 1878.

*Stipecoma parabolica* Miers, Apoc. So. Am. 137. 1878.

*Stipecoma peltata* (Vell.) Miers, Apoc. So. Am. 134. 1878.

*Stipecoma plicata* (A. DC.) Miers, Apoc. So. Am. 134. 1878 (*Echites plicata* A. DC. in DC. Prodr. 8: 454. 1844).

*Stipecoma pulchra* Miers, Apoc. So. Am. 135. pl. 18. 1878.

*Stipecoma speciosa* Miers, Apoc. So. Am. 136. 1878.

#### XV. ANGADENIA Miers, char. emend.

**Angadenia** Miers, Apoc. So. Am. 173. 1878, in part.

Lactescent, suffruticose or suffrutescent undershrubs. Stems erect, decumbent, or volubile, terete; branches alternate. Leaves opposite, petiolate to sessile, coriaceous to subcoriaceous, eglandular, entire, penninerved, the petioles somewhat girdling at the node into a slightly dilated, minutely appendiculate, stipular ring. Inflorescence lateral, infrequently terminal, alternate, scorpioid; peduncle simple or dichotomously compound at the base, usually more or less conspicuously flexuous. Flowers white to pale yellow. Calyx 5-parted, the lobes equal, imbricated, cleft nearly to the receptacle, bearing within 1-2 alternate squamellae. Corolla infundibuliform,



the tube straight, narrowly cylindrical below, somewhat below midway staminiferous and abruptly dilated into the broad, campanulate or tubular throat, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, inserted slightly below midway within the corolla-tube, wholly included; anthers connivent and agglutinated to the stigma, consisting of 2 apically convergent, basally protuberant sporangia borne ventrally near the apex of an enlarged, sagittate, acutely 2-auriculate connective; pollen granular. Carpels 2, united at the apex by an elongate, stylar shaft surmounted by the fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, usually concrescent, occasionally more or less separate. Follicles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, narrowly rostrate, apically comose seeds.

Type species: *Angadenia Berterii* (A. DC.) Miers, Apoc. So. Am. 180. 1878.

#### KEY TO THE SPECIES

- a. Corolla 3.7–4.5 cm. long, the throat tubular; inflorescence usually dichotomous below.....1. *A. Lindeniana*  
 aa. Corolla 2.5–3.4 cm. long, the throat conical to campanulate; inflorescence usually simple.....2. *A. Berterii*

1. *Angadenia Lindeniana* (Muell.-Arg.) Miers, Apoc. So. Am. 180. 1878.

*Rhabdadenia Lindeniana* Muell.-Arg. Linnaea 30: 437. 1860.

*Rhabdadenia Lindeniana* Muell.-Arg.  $\beta$  *angustifolia* Muell.-Arg. loc. cit. 438. 1860.

*Echites Lindeniana* (Muell.-Arg.) Griseb. Cat. Pl. Cub. 173. 1866.

Suffruticose or suffrutescent lianas; stems relatively slender, sparsely pilosulose to glabrate; leaves opposite, distinctly petiolate, broadly elliptic to oblong-lanceolate, apex acuminate, base obtuse, 2.0–6.5 cm. long, 1.5–3.0 cm. broad, firmly membranaceous, glabrous throughout, or very sparsely pilosulose when young, nitidulous above, opaque beneath; petioles 0.5–0.8 cm. long, glabrous or glabrate; inflorescence lateral, or infre-

quently subterminal, scorpioid, usually dichotomous below, bearing 6–18 showy, cream-colored flowers; peduncle usually about twice surpassing the subtending leaves, glabrous, or rarely very minutely puberulent; pedicels 1.0–1.2 cm. long, somewhat accrescent in fruit, glabrous or essentially so; bracts scarious, minutely ovate-lanceolate; calyx-lobes ovate-lanceolate, acuminate, 0.3–0.4 cm. long, scarious, glabrous, the squamellae 2–3; corolla infundibuliform, glabrous without, the proper-tube 0.7–1.3 cm. long, about 0.2–0.25 cm. in diameter at the base, the throat tubular, 1.5–2.0 cm. long, about 0.6–0.8 cm. in diameter at the orifice, the lobes obliquely obovate, 1.2–1.5 cm. long, widely spreading; anthers oblong-elliptic, narrowly sagittate, 0.45–0.5 cm. long, glabrous or essentially so; ovary ovoid, about 0.15 cm. long, glabrous; nectaries conerescent or essentially so, nearly twice surpassing the ovary; stigma about 0.1 cm. long; mature follicles unknown.

CUBA: MATANZAS: Arroyo Grande ad Jagüey, alt. 600 m., April, 1889, *Eggers 5297* (B, US); ORIENTE: wooded hills, vicinity of Santiago, March 10–25, 1912, *Britton Britton & Cowell 13848* (MBG, NY); in dense woods, exact locality lacking, July 21, 1859, *Wright 1376* (S, V); DATA INCOMPLETE: *Swartz s.n.* (S); *Linden 1699* (V).

JAMAICA: upper slopes of Mt. Diablo, alt. 500–800 m., Febr. 25–28, 1920, *Maxon & Killip 394* (US).

Relegation of *Maxon & Killip 394* to this species is not made with great assurance, as the corolla, preserved in only one instance, is much narrower, with respect to both proper-tube and throat, than in the Cuban specimens. Furthermore, it must be recalled that the apocynaceous floras of Cuba and Jamaica, at least in the highlands, are ordinarily specifically distinct.

**2. *Angadenia Berterii* (A. DC.) Miers, Apoc. So. Am. 180. 1878.**

*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844.

*Echites Sagraei* A. DC. loc. cit. 450. 1844.

*Echites ferruginea* A. Rich. in Sagra, Hist. Cuba 11: 92. 1850.

*Rhabdadenia Berteri* (A. DC.) Muell.-Arg. Linnaea 30: 435. 1860.

*Rhabdadenia Sagraei* (A. DC.) Muell.-Arg. loc. cit. 1860.

*Rhabdadenia cubensis* Muell.-Arg. loc. cit. 1860.

*Echites cubensis* (Muell.-Arg.) Griseb. Cat. Pl. Cub. 172. 1866.

*Angadenia Sagraei* (A. DC.) Miers, loc. cit. 181. 1878.

*Angadenia Havanensis* Miers, loc. cit. 1878.

*Angadenia Cubensis* (Muell.-Arg.) Miers, loc. cit. 182. 1878, where erroneously referred to Grisebach.

*Secondatia ferruginea* (A. Rich.) Miers, loc. cit. 227. 1878.

*Rhabdadenia corallicola* Small, Bull. N. Y. Bot. Gard. 3: 434. 1905.

Suffrutescent lianas, not rarely erect or suberect in their northern range; stems sparsely pilosulose to glabrate; leaves opposite, shortly petiolate to subsessile, ovate-elliptic to oblong-linear, apex acuminate to obtuse, not infrequently mucronulate, base obtuse, rarely obscurely cordate, 1–7 cm. long, 0.3–2.0 cm. broad, membranaceous to subcoriaceous, above glabrous, usually somewhat nitidulous, beneath opaque, glabrous, or minutely puberulent along the midrib; petioles 0.1–0.5 cm. long, occasionally essentially suppressed; inflorescence lateral in voluble specimens, subterminal to terminal in erect specimens, scorpioid, usually simple, infrequently dichotomous, bearing 5–30 cream-colored or yellowish flowers; peduncle twice or more surpassing the subtending leaves, glabrous to very minutely puberulent; pedicels 1.0–1.5 cm. long, glabrous to very minutely puberulent; bracts lanceolate, 0.1 cm. long or less, scarious; calyx-lobes ovate-lanceolate, acuminate, 0.3–0.5 cm. long, scarious, glabrous to very minutely puberulent-papillate without, the squamellae 1–2–3; corolla infundibuliform, glabrous to very indefinitely papillate without, the proper-tube 0.5–0.8 cm. long, about 0.2 cm. in diameter at the base, the throat broadly conical to campanulate, 1.0–1.5 cm. long, about 0.5–0.9 cm. in diameter at the orifice, the lobes obliquely obovate-dolabriform to subreniform-dolabriform, 1.0–1.3 cm. long, widely spreading; anthers subtrigonal, obtuse to acute, narrowly sagittate, 0.3–0.4 cm. long, indefinitely puberulent-papillate dorsally; ovary ovoid, about 0.1 cm. long,

glabrous; nectaries concrescent, about equalling the ovary, extremely variable and not infrequently more or less separate; stigma about 0.1 cm. long; follicles slender, divaricate, continuous, 5–10 cm. long, glabrous; seeds 0.5 cm. long, the pale yellowish coma about 2 cm. long.

UNITED STATES: FLORIDA: Miami, Dade Co., June, 1877, *Garber 11957* (MBG); pinelands, Miami, April 30, 1930, *Duckett s.n.* (MBG); in dry sandy marl, Goulds, Jan. 12, 1930, *Moldenke 399a* (MBG, NY); Big Pine Key, May, 1891, *Simpson 251* (US).

BAHAMA ISLANDS: near Nassau, April 25, 1903, *Curtiss 178* (MBG, US); in pinetis, New Providence, Febr. 28, 1888, *Eggers 4315* (US).

CUBA: ISLA DE PINOS: near Nueva Gerona, March 10–April 2, 1904, *Curtiss 395* (MBG); PINAR DEL RIO: palm barrens, west of Guane, Nov. 21–22, 1911, *Shafer 10428* (MBG, US); St. Yago de Cuba [Santiago], 1844, *Linden 2167* (V); mountains near El Guama, among grass on hillside, March 9, 1900, *Palmer & Riley 207* (US); trailing through bushes of sand swamp near seashore, near Coloma, March 18, 1900, *Palmer & Riley 337* (US); HABANA: Guanabacoa, date lacking, *Poeppig 537* (V); DATA INCOMPLETE: *Wright 2955* (MBG, S, V); *Sagra s.n.* (V).

HISPANIOLA: SANTO DOMINGO: in sylvis, alt. 100 m., April 26, 1887, *Eggers 1636* (B, US); La Jina, Distr. Moncion, Prov. Monte Cristy, April 19, 1933, *Valeur 978* (MBG).

The specimens from Santo Domingo demonstrate something of a transition to *A. Lindeniana* in the shape of the corolla-throat, which is nearly subtubular. The anthers are subtriangular, however, as in specimens of *A. Berterii* as interpreted above, from Cuba, the Bahamas, and Florida. This species is bewildering in its variations, particularly with regard to posture and shape of foliage. It would doubtless be indiscrete to segregate upon the present state of our knowledge.

The genus *Angadenia* as conceived by Miers is a hodge-podge of various elements, chiefly referable to *Odontadenia*, as the following list of excluded species testifies. After the removal of numerous species included within it by Miers but more properly referable to older genera, a distinct element centering about *Echites Berterii* A. DC. and *Rhabdadenia Lindeniana* Muell.-Arg. remains as a residue of manifestly related entities which form the genus *Angadenia* as here emended. As outlined by Mueller (loc. cit. 1860), these species differ from *Rhabdadenia* chiefly in the presence of calycine squamellae, although certain poorly defined characters of general aspect

might be mentioned in support of their segregation, among the more prominent of which is the extensive, zig-zag, scorpioid inflorescence of the former.

#### EXCLUDED SPECIES

*Angadenia Almadensis* (Stadelm.) Miers, Apoc. So. Am. 179. 1878 (*Echites almadensis* Stadelm. Flora 24<sup>1</sup>: Beibl. 28. 1841) = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792, not R. & P.).

*Angadenia Amazonica* (Stadelm.) Miers, Apoc. So. Am. 175. 1878 (*Echites amazonica* Stadelm. Flora 24<sup>1</sup>: Beibl. 50. 1841) = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932 (*Echites verrucosa* R. & S. Syst. 4: 795. 1819).

*Angadenia cognata* (Stadelm.) Miers, Apoc. So. Am. 176. 1878 (*Echites cognata* Stadelm. Flora 24<sup>1</sup>: Beibl. 79. 1841) = **Odontadenia cognata** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 546. 1931.

*Angadenia coriacea* (Benth.) Miers, Apoc. So. Am. 177. 1878 (*Echites coriacea* Benth. in Hook. Jour. Bot. 3: 249. 1841) = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860 (*Echites geminata* R. & S. Syst. 4: 795. 1819).

*Angadenia Cururu* (Mart.) Miers, Apoc. So. Am. 175. 1878 (*Echites Cururu* Mart. in Buchn. Rep. Pharm. 101. 1830) = **Odontadenia puncticulosa** (A. Rich.) Pulle, Enum. Pl. Surinam 383. 1906 (*Echites puncticulosa* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Angadenia elegans* (Benth.) Miers, Apoc. So. Am. 178. 1878 (*Echites elegans* Benth. in Hook. Jour. Bot. 3: 249. 1841) = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860 (*Echites geminata* R. & S. Syst. 4: 795. 1819).

*Angadenia elliptica* Miers, Apoc. So. Am. 180. 1878. Based upon *Gardner 2663* collected at Paranagua, State of Parana, Brazil, which has not been available for study. The unusually meager description appears to refer to **Odontadenia gracilipes**

(Stadelm.) Woodson, Ann. Mo. Bot. Gard. 22: 294. 1935 (*Echites gracilipes* Stadelm. Flora 24<sup>1</sup>: Beibl. 22. 1841), which is at present known only from the State of Minas Geraes.

*Angadenia geminata* (R. & S.) Miers, Apoc. So. Am. 178. 1878 (*Echites geminata* R. & S. Syst. 4: 795. 1819) = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860.

*Angadenia grandifolia* (Stadelm.) Miers, Apoc. So. Am. 175. 1878 (*Echites Cururu* Mart. var.  $\beta$  *grandifolia* Stadelm. Flora 24<sup>1</sup>: Beibl. 79. 1841) = **Odontadenia puncticulosa** (A. Rich.) Pulle, Enum. Pl. Surinam, 383. 1906 (*Echites puncticulosa* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Angadenia hypoglauca* (Stadelm.) Miers, Apoc. So. Am. 173. 1878 (*Echites hypoglauca* Stadelm. Flora 24<sup>1</sup>: Beibl. 23. 1841) = **Odontadenia hypoglauca** (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860.

*Angadenia latifolia* (Muell.-Arg.) Miers, Apoc. So. Am. 176. 1878 (*Anisolobus amazonicus* (Stadelm.) Muell.-Arg.  $\beta$  *latifolius* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 114. 1860) = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932 (*Echites verrucosa* R. & S. Syst. 4: 795. 1819).

*Angadenia majuscula* Miers, Apoc. So. Am. 174. 1878 = **Odontadenia hypoglauca** (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860 (*Echites hypoglauca* Stadelm. Flora 24<sup>1</sup>: Beibl. 23. 1841).

*Angadenia nitida* (Vahl) Miers, Apoc. So. Am. 177. 1878 (*Echites nitida* Vahl, Elog. 2: 19. pl. 13. 1798) = **Odontadenia nitida** (Vahl) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860.

*Angadenia pandurata* (A. DC.) Miers, Apoc. So. Am. 182. 1878 (*Echites pandurata* A. DC. in DC. Prodr. 8: 458. 1844) = **Fernaldia pandurata** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

*Angadenia Pöppigii* (Muell.-Arg.) Miers, Apoc. So. Am. 179. 1878 (*Odontadenia Poeppigii* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860) = **Odontadenia geminata** (R. & S.) Muell.-Arg. loc. cit. 119. 1860 (*Echites geminata* R. & S. Syst. 4: 795. 1819).

*Angadenia Prieurii* (A. DC.) Miers, Apoc. So. Am. 182. 1878, err. typ. (*Echites Prieurei* A. DC. in DC. Prodr. 8: 458. 1844) = **Mandevilla subspicata** (Vahl) Mgf. Rec. Trav. Bot. Néerl. 22: 380. 1926 (*Echites subspicata* Vahl, Eclog. Am. 2: 18. 1798).

*Angadenia pruinosa* Miers, Apoc. So. Am. 177. 1878. Based upon *Gardner 2232*, collected at Oeiras, Para, Brazil. Miers expressed the opinion (loc. cit.) that "The follicles and seeds exactly correspond with those of *A. hebecarpus*, showing that it belongs to this genus." Miers evidently referred to **Odontadenia lutea** (Vell.) Mgf. in Fedde, Rep. Sp. Nov. 20: 24. 1924 (*Echites lutea* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 25. 1827) = *Anisolobus hebecarpus* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 111. pl. 33. 1860, although he did not formally transfer that species to *Angadenia*, doubtless through oversight.

*Angadenia reticulata* Miers, Apoc. So. Am. 179. 1878 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Angadenia Sprucei* (Muell.-Arg.) Miers, Apoc. So. Am. 176. 1878 (*Anisolobus Sprucei* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 114. 1860) = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932 (*Echites verrucosa* R. & S. Syst. 4: 795. 1819).

*Angadenia sylvestris* (A. DC.) Miers, Apoc. So. Am. 174. 1878 (*Echites sylvestris* A. DC. in DC. Prodr. 8: 464. 1844) = **Odontadenia Hoffmannseggiana** (Steud.) Woodson, ex Gleason & A. C. Smith, Bull. Torrey Bot. Club 60: 392. 1933 (*Echites Hoffmannseggiana* Steud. Nomencl. ed. 2. 1: 539. 1840).

*Angadenia Valenzuelana* (A. Rich.) Miers, Apoc. So. Am. 181. 1878 (*Echites Valenzuelana* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850) = **Neobracea Valenzuelana** (A. Rich.) Urb. Symb. Ant. 9: 241. 1924.

## XVI. URECHITES Muell.-Arg.

**Urechites** Muell.-Arg. Bot. Zeit. 18: 22. 1860; Benth. & Hook. Gen. Pl. 2: 727. 1876; Miers, Apoc. So. Am. 124. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Chariomma* Miers, loc. cit. 110. 1878.

Lactescent fruticose or suffruticose lianas. Stems volubile, infrequently suberect, terete; branches alternate, or opposite below. Leaves opposite or rarely subverticillate, petiolate, membranaceous to subcoriaceous, eglandular, entire, penninerved, the petioles subtended by an inconspicuously appendiculate, interpetiolar, stipular ring. Inflorescence lateral to subterminal or terminal, simply scorpioid, bearing few to many showy, yellowish or cream-colored flowers; peduncle straight to slightly flexuous, conspicuously bracteate. Calyx 5-parted, the lobes equal to subequal, imbricated, cleft nearly to the receptacle, bearing within paired alternate, or numerous indefinitely distributed squamellae. Corolla infundibuliform, the tube straight, about midway, or somewhat lower, staminiferous, and abruptly dilated into a broad, tubular throat, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, wholly included, or the appendages somewhat exerted; anthers connivent and agglutinated to the stigma, consisting of 2 apically convergent, basally protuberant sporangia borne ventrally near the apex of an enlarged, sagittate, acutely 2-auriculated connective bearing, except rarely, conspicuous, spirally coiled, linear, apical appendages; pollen granular. Carpels 2, united at the apex by an elongate, stylar shaft surmounted by the capitate-fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, conerescent or essentially separate. Follicles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, narrowly rostrate, apically comose seeds mingled with subtending, subscaphiform, placental chaff.

Type species: *Urechites lutea* (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907.

#### KEY TO THE SPECIES

- a. Calyx-lobes linear-lanceolate, acuminate, usually equalling or slightly surpassing the proper-tube of the corolla; squamellae numerous, indefinitely distributed; nectaries essentially separate; plants of southern peninsular Florida, the Bahama Islands, the Antilles, rarely locally in northern Atlantic coastal Central America.....1. *U. lutea*



- aa. Calyx lobes ovate, obtuse, much shorter than the proper-tube of the corolla; squamellae paired, alternate with the calyx-lobes; nectaries concentric; plants of northern Central America.....3. *U. Andrieuxii*

1. *Urechites lutea* (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907.

*Vinca lutea* L. Cent. II. Pl. 12. 1756.

*Echites suberecta* Jacq. Enum. Pl. Carib. 13. 1760.

*Echites domingensis* Jacq. Ic. Rar. 1: 6. pl. 26. 1782.

*Echites heterophylla* J. F. Gmel. Syst. 2: 437. 1791, not Miq.

*Echites barbata* Desv. ex Ham. Prodr. 30. 1825.

*Echites Catesbaei* G. Don, Gen. Hist. 4: 74. 1838.

*Haemadictyon suberectum* (Jacq.) G. Don, loc. cit. 83. 1838.

*Neriandra suberecta* (Jacq.) A. DC. in DC. Prodr. 8: 422. 1844.

*Dipladenia flava* Hook. Bot. Mag. 79: pl. 4702. 1853.

*Echites Peltieri* Loud. Encycl. 1541. 1855, nom. nud. in synon.

*Echites Andrewsii* Chapm. Fl. So. U. S. 359. 1860.

*Urechites Jaegeri* Muell.-Arg. Linnaea 30: 443. 1860.

*Urechites suberecta* (Jacq.) Muell.-Arg. loc. cit. 444. 1860; Miers, Apoc. So. Am. 125. 1878.

*Urechites suberecta* (Jacq.) Muell.-Arg.  $\beta$  *glabrata* Muell.-Arg. loc. cit. 444. 1860.

*Urechites suberecta* (Jacq.) Muell.-Arg.  $\gamma$  *rotundifolia* Muell.-Arg. loc. cit. 1860.

*Echites neriandra* Griseb. Fl. Brit. W. I. 415. 1861.

*Echites jamaicensis* Griseb. loc. cit. 416. 1861.

*Chariomma surrecta* Miers, loc. cit. 111. 1878.

*Nerium sarmentosum* P. Browne, ex Miers, loc. cit. 111. 1878, err. in synon.

*Chariomma Domingensis* (Jacq.) Miers, loc. cit. 112. 1878.

*Chariomma mucronulata* Miers, loc. cit. 112. 1878.

*Chariomma flava* (Hook.) Miers, loc. cit. 113. 1878.

*Chariomma verticillata* Miers, loc. cit. 1878.

*Chariomma scandens* Miers, loc. cit. 114. 1878.

*Rhabdadenia laxiflora* Miers, loc. cit. 120. 1878.

*Rhabdadenia barbata* (Desv.) Miers, loc. cit. 123. 1878.

*Laubertia urechites* Griseb. ex Miers, loc. cit. 125. 1878,  
err in synon.

*Urechites Neriandra* Griseb. ex Miers, loc. cit. 126. 1878,  
err in synon.

*Laseguea Jaegeri* (Muell.-Arg.) Miers, loc. cit. 254. 1878.

*Laseguea pubiflora* Miers, loc. cit. 253. 1878.

*Echites obovata* Sesse & Moc. Fl. Mex. 43. 1887, not Nees,  
fide Urb. Symb. Ant. 4: 496. 1903.

*Urechites Andrewsii* (Chapm.) Small, Fl. Southeast. U. S.  
936. 1903.

*Urechites dolicantha* Urb. Symb. Ant. 6: 38. 1909.

*Urechites pinetorum* Small, Addisonia 4: 21. pl. 131.  
1919.

*Urechites lutea* (L.) Britton var. *angustifolia* Ekm. & Hel-  
wig, Arkiv f. Bot. 22A<sup>10</sup>: 46. 1929.

An extremely variable species. Stems volubile or occasionally suberect, relatively stout, glabrous to densely pilose; leaves opposite, shortly petiolate, oblong-linear to subrotund, apex shortly acuminate to obtuse or rounded, base obtuse to obscurely cordate, 3–9 cm. long, 0.5–6.0 cm. broad, membranaceous to subcoriaceous, either surface glabrous to pilose; petioles 0.2–1.2 cm. long; inflorescence lateral, alternate, occasionally subterminal or terminal, the peduncle usually somewhat surpassing the subtending leaves, occasionally somewhat shorter, generally more or less pilose, rarely glabrate, bearing few to relatively many handsome, yellowish or cream-colored flowers; pedicels 1.0–1.5 cm. long, usually somewhat pilosulose, less frequently glabrate; bracts foliaceous, ovate to ovate-lanceolate, 0.2–0.8 cm. long; calyx-lobes linear-lanceolate, acuminate, 0.8–1.7 cm. long, usually more or less pilose or pilosulose, infrequently glabrate, the squamellae numerous, indefinitely distributed; corolla infundibuliform, glabrous to laxly pilose without, the proper-tube rather narrowly cylindrical, 0.6–1.5 cm. long, about 0.2 cm. in diameter at the base, the throat broadly tubular to tubular-subconical, 1.5–3.5 cm. long, about

0.8–1.2 cm. in diameter at the orifice, the lobes obliquely obovate, 1.8–3.0 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers 0.5–0.55 cm. long, minutely puberulent dorsally, the apical appendages 1.3–1.7 cm. long, usually more or less exserted; ovary ovoid, about 0.1 cm. long, glabrous or essentially so; nectaries essentially separate or more or less concrescent at the base, about equaling the ovary; stigma 0.125 cm. long; follicles relatively stout, acuminate, continuous, 8–20 cm. long, glabrous to more or less densely pilosulose; seeds 0.7–1.1 cm. long, the pale tawny coma 1.5–3.0 cm. long, the placental chaff 1.0–1.3 cm. long.

UNITED STATES: FLORIDA: shrub on midden, Coconut, Lee Co., Febr. 19, 1930, *Moldenke 5784* (NY); in dry sandy soil along roadside, near Caxambos, Collier Co., April 17, 1930, *Moldenke 1006a* (NY); rich thickets, Upper Metacombe Key, in coral soil, July, year lacking, *Curtiss 2267* (MBG, NY, US); pinelands, west of Coconut Grove, May 15, 1918, *Small 8786* (NY); in pinelands, between Homestead and Camp Jackson, May 4–11, 1904, *Small & Wilson 1756* (NY); hammocks, Big Pine Key, Dec. 2, 1912, *Small 3995* (NY); pinelands between Miami and Kendall Station, Nov. 5, 1906, *Small & Carter 2654* (NY); hammocks, Grassy Key, Jan. 28–29, 1909, *Small & Carter 3116* (NY); Key West, Aug., 1887, *Garber s.n.* (US).

BAHAMA ISLANDS: near Nassau, New Providence, April–May, 1903, *Curtiss 172* (MBG, NY, US); coppice, near Deep Creek, Long Bay Cays section, Andros, Jan. 20–22, 1910, *Small & Carter 8605* (NY, US); scrub, Mathew Town, Oct. 10, 1904, *Nash & Taylor 898* (NY); scrublands, Cockburn Town and vicinity, Watling's, March 12–13, 1907, *Britton & Millspaugh 6093* (NY); Spring Point, Acklin's, Dec. 21, 1905–Jan. 6, 1906, *Brace 4373* (NY); coppice, Grand Turk, Aug. 27–Sept. 1, 1905, *Nash & Taylor 3773* (NY, US); West End, Great Bahama, April 16–May 8, 1905, *Brace 3601* (NY); Crooked Is., Nov., 1881, *Hitchcock s.n.* (MBG); Governor's Harbor, Nov. 15, 1890, *Hitchcock s.n.* (MBG).

CUBA: PINAR DEL RIO: climbing over bushes of sandy swamp near the shore, near Coloma, March 18, 1900, *Palmer & Riley 364* (NY, US); oak grove north of San Diego de los Baños, June 28, 1915, *Leon 5108* (NY); ISLA DE PINOS: swamp, climber over bushes, near Nueva Gerona, July 5, 1900, *Palmer & Riley 1010* (US); on coral soil, north of Caleta Grande, May 22, 1910, *Jennings 463B* (NY); HABANA: in swamp near seashore, near Playa de Marianao, June 17, 1900, *Palmer & Riley 833* (US); near Morro Castle, May 20, 1908, *Leon 713* (NY); MATANZAS: Cardenas, Sept. 1, 1903, *Britton & Wilson 190* (NY); SANTA CLARA: Cienegueta, May 9, 1895, *Combs 13* (MBG, US); coastal thicket, Rio Arimao, March 22, 1910, *Britton & Wilson 5809* (NY); CAMAGUEY: vicinity of La Gloria, Febr. 4, 1909, *Shafer 297* (NY, US); Cayo Paredon Grande, Oct. 25, 1909, *Shafer 2748* (NY, US); ORIENTE: woods, Alto Cedro to Paso Estancia, April 28, 1909, *Shafer 1624* (NY, US); coastal thicket, Fisherman's Point, Guantanamo Bay, March 17–30, 1909, *Britton 2110* (NY, US).

JAMAICA: roadside, Constant Spring, Aug. 29–31, 1907, *Britton 961* (NY);

banks, Balaclava, Cockpit Country, Sept. 13–18, 1906, *Britton 433* (NY); climbing on roadside banks, vicinity of Montego Bay, March 28–30, 1920, *Mason & Killip 1440* (NY, US); rocks, Navy Island, July 14, 1897, *Fredholm 3163* (US); climbing over shrubs, Holly Mts., Mt. Diablo, alt. 3000 ft., Aug. 31, 1905, *Harris 9007* (NY); Lititz Savanna, July 7, 1914, *Harris 11732* (MBG, NY, US); near Castleton, alt. 500 ft., June 26, 1915, *Harris 18085* (MBG, NY, US).

HISPANIOLA: SANTO DOMINGO: sandy roadside, Haina, April 3, 1921, *Faris 119* (US); district of Moncion, Prov. Monte Cristi, Aug. 12, 1929, *Valeur 175* (MBG, US); Azua, March, 1913, *Rose Fitch & Russell 3960* (US); Paradis, pr. Barahona, in fruticetis litoralibus, Dec., 1909, *Tuerckheim 2688* (NY, US); HAITI: windswept rocky beach east of Cabaret, Jan. 14, 1929, *Leonard & Leonard 11986* (US); dry thickets east of harbor, vicinity of La Vallee, Tortue Island, Jan. 5, 1929, *Leonard & Leonard 11642* (US); Massif de la Hotte, Jeremie, between Sources-Chaudees and Source-Cahouane, July 4, 1928, *Ekman 10224* (US); Bayeux, near Port Margot, Aug. 4, 1903, *Nash 135* (NY); La Brande, alt. 700 ft., Aug. 14, 1905, *Nash & Taylor 1633* (NY).

PORTO RICO: Salinas de Cabo-Rajo, in sylvis litoralibus, Febr. 8, 1885, *Sintenis 2730* (US); in declivibus, Cabeza de San Juan, Sept. 14, 1885, *Sintenis 1891* (US); climbing over bushes in thicket, sandy shore, Playa de Esperanza, Vieques Island, Febr. 7, 1914, *Shafer 2737* (NY, US); sandy plain, Icacos Cay, Jan. 30, 1923, *Britton 7159* (NY).

VIRGIN ISLANDS: ST. THOMAS: rocky point, Cowell Point, Jan. 31–Febr. 4, 1913, *Britton & Shafer 91* (NY, US); ST. CROIX: Grenard, Nov. 14, 1925, *Thompson 1005* (NY).

LEEWARD ISLANDS: TORTOLA: coastal thicket, Fish Bay to Road Town, Febr. 13–17, 1913, *Britton & Shafer 911* (NY, US); ANEGADA: sandy plain, West End, Febr. 19–20, 1913, *Britton & Fishlock 946* (NY, US); ST. MARTIN: March 28, 1926, *Goodwin & Goodwin 4* (NY); ANGUILLA, April 6, 1926, *Goodwin & Goodwin 16* (NY); ST. CHRISTOPHER: gulch, Canada Estate, Sept. 8–Oct. 5, 1901, *Britton & Cowell 365* (NY).

Also reported from the vicinity of Santa Marta, Colombia, by Purdie. This species is very unstable, even in such an important character as the linear appendages of the anther tips, which may occasionally be totally lacking, or extremely short. This is apparently the most frequently collected of the American Echitoideae, and space permits only the greatly abridged representation cited above. Although segregation may appear an attractive solution of the vexatious variability, a wide selection of specimens, such as that which has been available for these studies, should prove an effective deterrent.

**2. *Urechites Andrieuxii* Muell.-Arg. *Linnaea* 30: 442. 1860; Miers, *Apoc. So. Am.* 125. 1878.**

Stems relatively stout, minutely hirtellous when young,

eventually becoming glabrate; leaves opposite, petiolate, oblong- to ovate- or obovate-elliptic, apex rather shortly acuminate, base obtuse to rounded, 5–12 cm. long, 2.5–7.0 cm. broad, membranaceous to subcoriaceous, glabrous above, glabrous to very finely puberulent beneath; petioles 0.8–2.0 cm. long; inflorescence lateral, alternate, the peduncle usually somewhat surpassing the subtending leaves, bearing few to numerous handsome, yellow or cream colored flowers, glabrous to very inconspicuously puberulent; pedicels 1.5–2.2 cm. long, glabrous or essentially so; bracts minute, scarious, caducous; corolla infundibuliform, glabrous without, the proper-tube 1.0–1.5 cm. long, about 0.3 cm. in diameter at the base, slightly constricted toward the insertion of the stamens, the throat broadly tubular to subtubular, 2.5–3.0 cm. long, 0.5–0.8 cm. in diameter at the orifice, the lobes obliquely obovate, 1.5–2.3 cm. long, spreading; stamens inserted at the base of the corolla-throat, the anthers 0.6–0.7 cm. long, essentially glabrous to very minutely puberulent-papillate dorsally, the apical appendages linear, 0.7–0.9 cm. long; ovary ovoid, 0.15 cm. long, glabrous; nectaries conerescent, about twice surpassing the ovary; stigma 0.2 cm. long; calyx-lobes ovate, obtuse, 0.4–0.5 cm. long, glabrous or very indefinitely papillate, the squamellae in alternate pairs; follicles relatively stout, acuminate, falcate, continuous, 15–28 cm. long, glabrous; seeds 1.5–1.8 cm. long (including the rostrum), the pale tawny coma 2.5–3.5 cm. long.

MEXICO: CAMPECHE: over trees overhanging river, Champoton, July 7–15, 1932, *Steere 1918* (MBG); Tuxtepec, Dec. 3, 1931, *Lundell 843* (MBG).

BRITISH HONDURAS: occupied clearing, Belize, June, 1933, *Lundell 4056* (MBG); Jones Bank, March, 1933, *Lundell 4046* (MBG); San Andres, Corozal, July 11, 1933, *Lundell 4736* (MBG); Santa Rita, Oct., 1933, *Gentle 800* (MBG); Northern River, Dec., 1933, *Gentle 1037* (MBG); Honey Camp, Orange Walk, Nov., 1928, *Lundell LP38* (US); small climber growing in mangrove swamp, Stann Creek, Dec. 8, 1929, *Schipp 491* (MBG).

GUATEMALA: PETEN: La Libertad, May 31, 1933, *Lundell 3533* (MBG); Monte Polol, May 28, 1933, *Lundell 3445* (MBG); El Paso, common vine in low places, April 24, 1932, *Lundell 1524* (MBG); Santa Cruz, March 27–28, 1931, *Bartlett 12366* (MBG); ZACAPA: Gualan, alt. 620 ft., June 16, 1909, *Deam 6320* (MBG, NY).

The seminal rostrum of this species is much longer than that of *U. lutea*, and the placental chaff is less delicate, more defi-

nately scaphiform, and with much less tendency to scale from the placenta upon dehiscence of the follicles.

#### EXCLUDED SPECIES

*Urechites Karwinskii* Muell.-Arg. *Linnaea* 30: 440. 1860 = ***Fernaldia pandurata*** (A. DC.) Woodson, *Ann. Mo. Bot. Gard.* 19: 48. 1932 (*Echites pandurata* A. DC. in DC. *Prodr.* 8: 458. 1844).

#### XVII. RHABDADENIA Muell.-Arg.

***Rhabdadenia*** Muell.-Arg. in *Mart. Fl. Bras.* 6<sup>1</sup>: 173. 1860; Miers, *Apoc. So. Am.* 118. 1878; K. Sch. in *Engl. & Prantl, Nat. Pflanzenfam.* 4<sup>2</sup>: 170. 1895.

Lactescent, suffruticose or suffrutescent lianas. Stems voluble or rarely suberect, terete; branches usually opposite below, becoming alternate above. Leaves opposite, petiolate to subsessile, the blade coriaceous to membranaceous, entire, penninerved, eglandular; petioles somewhat girdling at the node into a rather inconspicuous, minutely appendiculate, stipular ring. Inflorescence a lateral or subterminal, alternate, greatly reduced, dichasial cyme, frequently uniflorous. Flowers pedicellate, subtended by a solitary bract. Corolla infundibuliform, the proper-tube straight, narrowly cylindrical, the throat conical or tubular, the limb actinomorphic, 5-parted, dextrorsely convolute, widely spreading. Calyx 5-parted, the lobes equal or subequal, cleft nearly to the receptacle, subeglandular within; stamens 5, epipetalous, the anthers coherent, consisting of 2 longitudinal, apically convergent, bilocular sporangia borne ventrally near the apex of an enlarged, sagittate, acutely biauriculate, dorsally pilose connective, the filament subcylindrical, puberulent, the pollen granular. Carpels 2, sessile or subinferior, apocarpous, united at the apex by an elongate, stylar shaft surmounted by the fusiform, apically pilose stigma; ovules many, anatropous, borne upon an axile, binate placenta. Nectaries 5, separate or somewhat concrescent at the base. Follicles 2, apocarpous, terete, continuous, dehiscing along the ventral suture, containing

many dry, subscaaphiform, rostrate, apically comose seeds; embryo straight, typically dicotyledonous.

Type species: *Rhabdadenia Pohlîi* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 174. 1860.

#### KEY TO THE SPECIES

- a. Corolla white, the throat conical, dilating continuously toward the orifice; leaves coriaceous or firmly chartaceous; plants of the Antilles, the Bahama Islands, southern Florida, and Central America, also locally in lowlands of northern South America.....1. *E. biflora*
- aa. Corolla pink to rose-colored, the throat tubular, not dilating toward the orifice or only slightly so; leaves membranaceous; species of South America.
  - b. Plants scatteringly pilose; calyx-lobes 0.2–0.4 cm. long, much shorter than the proper-tube of the corolla.....2. *E. macrostoma*
  - bb. Plants glabrous; calyx-lobes 0.8–1.25 cm. long, about equalling the length of the proper-tube of the corolla.....3. *E. Pohlîi*

1. *Rhabdadenia biflora* (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860; Miers, Apoc. So. Am. 121. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 170. 1895.

*Echites biflora* Jacq. Enum. Pl. Carib. 13. 1760; L. Sp. Pl. ed. 2. 307. 1762; Jacq. Select. Stirp. Am. Hist. 1: 30; 2: pl. 21. 1763; A. DC. in DC. Prodr. 8: 450. 1844.

*Echites paludosa* Vahl, Eclog. 2: 19. 1798; A. DC. loc. cit. 467. 1844.

*Erothostemon paludosum* (Vahl) G. Don, Gen. Hist. 4: 83. 1838; Miers, loc. cit. 241. 1878.

*Echites Ehrenbergii* Schlecht. Linnaea 26: 666. 1853.

*Echites Billbergii* Beurl. Vet. Akad. Handl. Stockh. 137. 1854 (1856).

*Rhabdadenia Ehrenbergii* (Schlecht.) Muell.-Arg. Linnaea 30: 454. 1860.

*Rhabdadenia paludosa* (Vahl) Miers, Apoc. So. Am. 119. 1878.

*Rhabdadenia nervosa* Miers, loc. cit. 122. 1878.

*Rhabdadenia cordata* Miers, loc. cit. 1878.

*Rhabdadenia macrantha* Donn. Sm. Bot. Gaz. 40: 7. 1905.

Glabrous, suffruticose lianas; stems terete, relatively stout; leaves opposite, petiolate, the blade coriaceous or firmly chartaceous, broadly obovate-oblong to lanceolate, apex usually

rather abruptly mucronulate, base obtuse, either surface yellowish-green, the upper somewhat nitidulous, 5–12 cm. long, 1.5–5.0 cm. broad, the petiole 1–2 cm. long; inflorescence lateral or rarely subterminal, cymose, the peduncle equalling or somewhat surpassing the length of the subtending leaves, bearing 1–5 white flowers clustered at the apex; pedicels 1.0–1.25 cm. long, somewhat accrescent in fruit, the subtending bracts scarious, minute; calyx-lobes subfoliaceous, broadly ovate-oblong, mucronulate, 0.1–0.9 cm. long; corolla infundibuliform, the proper-tube narrowly cylindrical, 1.5–2.0 cm. long, about 0.2 cm. in diameter at the base, somewhat constricted toward the insertion of the stamens, the throat conical, 2.0–3.0 cm. long, about 1.5 cm. in diameter at the orifice, the lobes broadly obovate, 2.0–2.5 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers elliptic-oblong, densely pilose dorsally, 0.5 cm. long; ovary ovoid, 0.2 cm. long, rather gradually produced into the style, glabrous; nectaries depressed-quadrate, essentially separate, about half equalling the length of the ovary; stigma 0.2 cm. long; mature follicles unknown.

UNITED STATES: FLORIDA: exact locality lacking, 1842–49, *Eugel 114* (MBG, BM); in sandy soil at edge of bay near Brickell Hammock, Miami, Dade Co., March 4, 1930, *Moldenke 725* (MBG, NY); salt marshes, Fort Myers, July–Aug., 1900, *Hitchcock 202* (MBG); Miami, June, 1877, *Garber s.n.* (MBG).

CUBA: exact locality lacking, 1860–64, *Wright 2954* (MBG); SANTA CLARA: Cienfuegos, Rio Damuji, May 23, 1895, *Combs 78* (MBG); data incomplete, *Sagra s.n.* (V).

JAMAICA: Port Antonio, Dec. 31, 1890, *Hitchcock s.n.* (MBG); Port Morant, Dec. 20, 1890, *Hitchcock s.n.* (MBG); GRAND CAYMAN: Jan., 1891, *Hitchcock s.n.* (MBG).

HISPANIOLA: HAITI: Grande Caymite, Aug. 20, 1927, *Eyerdam 321* (MBG); SANTO DOMINGO: Prov. Barahona, July, 1910, *Fuertes 220* (MBG).

PORTO RICO: prope Bayamon, in paludosis, March 23, 1885, *Sintenis 935* (S); Playa de Carmelita, in fruticetis paludosis prope marem, April, 1883, *Eggers 336* (V).

MEXICO: CAMPECHE: over shrubs in Pantel Aguada, Champoton, July 7–15, 1932, *Steere 1937* (MBG); YUCATAN: Port Silam, 1895, *Gaumer 653* (MBG); lagoon shores, Las Bocas de Silam, May, 1916, *Gaumer 23335* (MBG).

BRITISH HONDURAS: Stann Creek, common climber in swampy places along the coast, April 15, 1929, *Schipp 148* (MBG); mangrove swamp, Belize, March 11, 1933, *Lundell 1813* (MBG); Pueblo Nuevo, New River, July 17, 1933, *Lundell 4792* (MBG).



PANAMA: COLON: Porto Bello, April, 1826, *Billberg 254* (S); CANAL ZONE: Chagres, Jan.-March, 1850, *Fendler 257* (MBG).

COLOMBIA: MAGDALENA: Santa Marta, 1898-1901, *Smith 1664* (MBG); BOLIVAR: region of Barranquilla, April, 1935, *Elias 1291* (MBG).

BRITISH GUIANA: Kabakaburi, Pomeroon District, Febr. 10-15, 1923, *Crus 3274* (MBG); upper Rupununi River, near Dadanawa, May 30, 1922, *Crus 1417* (MBG).

FRENCH GUIANA: Cayenne, 1859, *Sagot 337* (V).

DUTCH GUIANA: Paramaribo, date lacking, *Wulfschlägel 324* (V).

BRAZIL: PARA: Caripi, juxta Para, Aug., 1849, *Spruce s.n.* (Camb., V); in *maritimis inundatis* ad Colares, May, 1832, *Poeppig 2946* (V); MARANHÃO: on lowland, border of river, Maracassume River region, Sept. 9, 1932, *Krukoff 1836* (MBG, NY); data incomplete, *Gardner 6060* (Camb., V).

**2. *Rhabdadenia macrostoma* (Benth.) Muell.-Arg.** *Linnaea* 30: 435. 1860; Miers, *Apoc. So. Am.* 123. 1878; K. Sch. in Engl. & Prantl, *Nat. Pflanzenfam.* 4<sup>2</sup>: 170. 1895.

*Echites macrostoma* Benth. in Hook. *Jour. Bot.* 3: 248. 1841; A. DC. in DC. *Prodr.* 8: 453. 1844.

Suffruticose or suffrutescent lianas; stems terete, scattering-ly pilose when young, eventually becoming glabrate; leaves opposite, petiolate, the blade membranaceous, obovate-oblong to broadly oblong-elliptic, apex rather abruptly mucronate, base obtuse to rounded, 3-6 cm. long, 1.5-3.5 cm. broad, upper surface minutely bullate-puberulent to glabrate, lower surface sparsely pilose along the midrib and veins, the petiole 0.3-0.5 cm. long, finely pilose to glabrate; cymes lateral, the peduncle about twice surpassing the length of the subtending leaves, bearing two pink or rose-colored flowers at the apex; pedicels 0.3-0.5 cm. long, somewhat accrescent in fruit, the subtending bracts scarious, lanceolate, minute; calyx-lobes scarious, linear-lanceolate, 0.2-0.4 cm. long, minutely and sparsely pilose to glabrate; corolla infundibuliform, the proper-tube narrowly cylindrical, 0.75-1.0 cm. long, about 0.1 cm. in diameter at the base, the throat broadly tubular, 3.0-3.5 cm. long, about 1 cm. in diameter at the orifice, the lobes broadly obovate, 1.5 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly oblong-lanceolate, 0.4 cm. long, pilose above; ovary oblongoid, 0.1 cm. long, rather gradually produced into the style, glabrous; stigma 0.2 cm. long; nectaries oblongoid, essentially separate, somewhat shorter

than the ovary; follicles terete, relatively slender, glabrous, 9–12 cm. long, seeds unknown.

BRITISH GUIANA: data incomplete, *Schomburgk 329* (Camb., V).

DUTCH GUIANA: locality lacking, 1846, *Hostmann 494, 712* (S); Paramaribo, date lacking, *Wulschlägel 326* (V).

BRAZIL: PARA: on varzea land, near Bocca do Paru, Aug. 28, 29, 1934, *Krukoff 5931* (NY); Parana do Ricardo, Aug. 28, 29, *Krukoff 5915* (NY).

PERU: LORETO: swampy thickets, Iquitos, alt. 100 m., Aug. 2–8, 1929, *Killip & Smith 26911* (MBG).

**3. *Rhabdadenia Pohl*** Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 174. pl. 52. 1860; Miers, Apoc. So. Am. 119. 1878: K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 170. 1895.

*Rhabdadenia Pohl* Muell.-Arg. var. *volubilis* Muell.-Arg. loc. cit. 1860.

*Rhabdadenia Pohl* Muell.-Arg. var. *suberecta* Muell.-Arg. loc. cit. 175. 1860.

*Rhabdadenia Pohl* Muell.-Arg. var. *latifolia* Muell.-Arg. loc. cit. 1860.

*Rhabdadenia latifolia* (Muell.-Arg.) Malme, Arkiv f. Bot. 21A<sup>6</sup>: 17. 1927.

*Rhabdadenia latifolia* (Muell.-Arg.) Malme var. *suberecta* (Muell.-Arg.) Malme, loc. cit. 18. 1927.

*Rhabdadenia mamorensis* Rusby, Mem. N. Y. Bot. Gard. 7: 326. 1927.

Glabrous, suffruticose or suffrutescent lianas, occasionally erect or suberect; stems relatively slender; leaves petiolate to sessile, the blade membranaceous, oblong-elliptic to linear, apex rather gradually acuminate, mucronulate, base narrowing from about the middle, obscurely auriculate, 5–12 cm. long, 0.75–3.0 cm. broad, either surface glabrous, the lower glaucescent, the petiole 0.25–1.0 cm. long, or essentially obsolete; cymes lateral to subterminal, the peduncle usually about twice surpassing the length of the subtending leaves, bearing 1–3 pink or rose-colored flowers at the apex; pedicels 0.5–1.0 cm. long, the subtending bracts filiform, minute; calyx-lobes narrowly oblong-lanceolate, minutely mucronulate, 0.8–1.25 cm. long; corolla infundibuliform, the proper-tube narrowly cylindrical, 0.75–1.0 cm. long, about 0.1 cm. in diameter at the base,

the throat rather broadly tubular, 2.5–3.5 cm. long, about 1 cm. in diameter at the orifice, the lobes broadly obovate, 1.5–2.0 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers narrowly lanceolate, 1.0–1.25 cm. long, sparsely pilosulose at the tip; ovary ovoid, 0.1 cm. long, rather gradually produced into the style, glabrous; stigma 0.4 cm. long; nectaries ovoid-oblongoid, separate, about equalling the length of the ovary; follicles unknown.

COLOMBIA: BOLIVAR: river marsh, Magangue, alt. 40–45 m., Jan. 18–19, 1918, *Pennell 3956* (MBG).

VENEZUELA: Sacupana, lower Orinoco, April, 1896, *Eusby & Squires 20* (MBG).

BRAZIL: PARANA: Piraquara, in paludosis, Jan. 7, 1909, *Dusen 7781* (MBG); exact locality lacking, Nov., 1916, *Brito 43* (US); RIO GRANDE DO SUL: Neu Württemberg, Estancia Coromel, Belisiano bei Lagão, Febr. 27, 1906, *Bornmüller 693* (M); same locality, Jan. 16, 1905, *Bornmüller 427* (M).

PARAGUAY: swamps, exact locality lacking, Dec. 8, 1928, *Jørgensen 3450* (MBG); in esteros, Frape, Jan. 5, 1929, *Jørgensen 4038* (MBG).

ARGENTINA: MISSIONES: San Ignacio, Jan., 1918, *Hauman 3591* (MBG).

This species varies greatly in its habit. Although always more or less twining in the northern portion of its range, it inclines strongly to the erect posture of such species as *Mandevilla erecta* (Vell.) Woodson. Perhaps such close relatives of normally twining congeners merit varietal or formal recognition, but our present evidence does not appear to warrant it.

#### EXCLUDED OR UNCERTAIN SPECIES

*Rhabdadenia barbata* (Desv.) Miers, Apoc. So. Am. 123. 1878 (*Echites barbata* Desv. ex Ham. Prodr. 30. 1825) = *Urechites lutea* (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Rhabdadenia Berterii* (A. DC.) Muell.-Arg. Linnaea 30: 446. 1860 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844) = *Angadenia Berterii* (A. DC.) Miers, Apoc. So. Am. 180. 1878.

*Rhabdadenia campestris* (Vell.) Miers, Apoc. So. Am. 121. 1878 (*Echites campestris* Vell. Fl. Flum. 113. 1830; Icon. 3: pl. 43. 1827) = *Mandevilla hirsuta* (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Rhabdadenia corallicola* Small, Bull. N. Y. Bot. Gard. 3: 434. 1905 = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

*Rhabdadenia cubensis* Muell.-Arg. Linnaea 30: 435. 1860 = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

*Rhabdadenia laxiflora* Miers, Apoc. So. Am. 120. 1878 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Rhabdadenia Lindeniana* Muell.-Arg. Linnaea 30: 437. 1860 = **Angadenia Lindeniana** (Muell.-Arg.) Miers, Apoc. So. Am. 180. 1878.

*Rhabdadenia madida* (Vell.) Miers, Apoc. So. Am. 121. 1878 (*Echites madida* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 42. 1827). Probably referable to a species of *Mandevilla*, such as *M. scabra* (R. & S.) K. Sch., in which the inflorescence is frequently reduced to few flowers.

*Rhabdadenia polyneura* Urb. Symb. Ant. 7: 337. 1912 = **Odontadenia polyneura** (Urb.) Woodson, Ann. Mo. Bot. Gard. 18: 546. 1931.

*Rhabdadenia Sagraei* (A. DC.) Muell.-Arg. Linnaea 30: 435. 1860 (*Echites Sagraei* A. DC. in DC. Prodr. 8: 450. 1844) = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

*Rhabdadenia Wrightiana* Muell.-Arg. Linnaea 30: 438. 1860 = **Neobraccia Valenzuelana** (A. Rich.) Urb. Symb. Ant. 9: 241. 1924 (*Echites Valenzuelana* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850).

### XVIII. *ELYTROPUS* Muell.-Arg.

**Elytropus** Muell.-Arg. Bot. Zeit. 18: 21. 1860; Benth. & Hook. Gen. Pl. 2: 728. 1876; Miers, Apoc. So. Am. 114. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 169. 1895.

Lactescent, suffruticose lianas. Stems terete, volubile, said to be suberect in some instances; branches alternate above, chiefly opposite below. Leaves opposite, shortly petiolate, pen-

ninerved, eglandular, the petioles subtended by 1-few inconspicuous, dentiform, adaxial stipular appendages. Inflorescence lateral, opposite, or infrequently alternate, determinate, 1-3-flowered, conspicuously bracteate. Calyx 5-parted, the lobes equal to sub-equal, cleft nearly to the receptacle, imbricated, eglandular. Corolla campanulate, the tube broad, ex-appendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia borne ventrally near the apex of an enlarged, narrowly sagittate connective; filaments separate; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the capitate-fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or essentially so. Follicles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, truncate, apically comose seeds.

Type species: *Elytropus chilensis* (A. DC.) Muell.-Arg. *Linnaea* 30: 440. 1860.

1. *Elytropus chilensis* (A. DC.) Muell.-Arg. *Linnaea* 30: 440. 1860. Miers, *Apoc. So. Am.* 115. 1878.

*Echites pubescens* Hook. & Arn. *Bot. Beechey Voy.* 34. 1841, not Willd.

*Echites Chilensis* A. DC. in DC. *Prodr.* 8: 468. 1844.

*Echites ptarmica* Poepp. *Nov. Gen.* 3: 69. *pl.* 278. 1845.

*Echites heterophylla* Miq. *Linnaea* 25: 653. 1852, not Gmel.

*Elytropus pubescens* (Hook. & Arn.) Miers, loc. cit. 114. 1878.

*Elytropus ptarmicus* (Poepp.) Miers, loc. cit. 115. 1878.

*Vinca sternutatoria* Poepp. ex Miers, loc. cit. 1878, nom. nud. in synon.

*Elytropus heterophyllus* (Miq.) Miers, loc. cit. 116. 1878.

Stems usually relatively stout, densely ferruginous-puberulent to glabrate; leaves opposite, shortly petiolate, ovate to oblong-elliptic, apex rather shortly acuminate, base obtuse to

rounded, 3.5–9.0 cm. long, 1.2–4.5 cm. broad, subcoriaceous, above glabrous, nitidulous, beneath opaque, persistently ferruginous-puberulent; petioles 0.5–1.0 cm. long, ferruginous-puberulent; inflorescence lateral, opposite, or infrequently alternate by the abortion of an opposite bud, much surpassed by the subtending leaves, 1–3-flowered; peduncle 0.3–0.7 cm. long, minutely puberulent to glabrate; bracts oblong-elliptic, 0.2–0.5 cm. long, somewhat foliaceous; pedicels 0.1–0.2 cm. long, minutely puberulent; calyx-lobes oblong-elliptic, acute, 0.55–0.8 cm. long, somewhat foliaceous, puberulent to pilosulose; corolla campanulate, glabrous without, the tube 0.5–0.9 cm. long, about 0.15–0.2 cm. in diameter at the base, 0.4–0.55 cm. in diameter at the orifice, the lobes obliquely ovate, shortly apiculate, 0.5–1.3 cm. long, spreading; stamens inserted near the base of the corolla-tube, the anthers barely included, oblong-sagittate, 0.5 cm. long, tips pilose; ovary ovoid, 0.07 cm. long, glabrous; stigma 0.15 cm. long; nectaries essentially separate, truncate, about equalling the ovary; follicles relatively stout, rather obscurely articulated, 15–20 cm. long, rather densely ferruginous-hirtellous; seeds 0.8–1.1 cm. long, the pale yellowish coma 3.0–3.5 cm. long.

CHILE: CHILOE: am Büschen schlingend, Piruquina, Oct. 22, 1931, *Gunckel 65* (MBG); data incomplete, Nov., 1925, *Joseph 3334* (US); LLANQUIHUE: Casa Panque, Dec., 1926, *Shannon & Shannon 28* (US); MALLECO: Cura Cautin, Nov., 1925, *Joseph 3397* (US); La Union, Oct. 25, 1931, *Behn 1179* (MBG); VALDIVIA: San Carlos, Oct. 5, 1931, *Gunckel 2361* (MBG); Loncoche, Sept., 1926, *Joseph 4408* (US); Panguipulli, Oct., 1923, *Joseph 2397* (US); Panguipulli, alt. 200 m., Oct., 1924, *Hollermayer 326* (MBG, NY, US); Ufergebüsch des Calle-Calle, Oct. 20, 1897, *Buchtien s.n.* (US); DATA INCOMPLETE: *Gay 384* (NY).

ARGENTINA: RIO NEGRO: Playa Bonita, region of Lago Nahuel Huapi, Nov. 1, 1928, *Cordoni s.n.* (MBG, US).

The relatively small cream-colored flowers are said to have a fragrance similar to that of Jasmine. Cordoni reports the flowers as violet or reddish.

#### EXCLUDED SPECIES

*Elytropus spectabilis* (Stadelm.) Miers, Apoc. So. Am. 116. 1878 (*Echites spectabilis* Stadelm. Flora 24<sup>1</sup>: Beibl. 44. 1841)

= *Macropharynx spectabilis* (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

### XIX. CYCLADENIA Benth.

*Cycladenia* Benth. Pl. Hartw. 322. 1849; Benth. & Hook. Gen. Pl. 2: 728. 1876; A. Gray, Syn. Fl. N. Am. ed. 1. 2<sup>1</sup>: 83. 1878; Miers, Apoc. So. Am. 263. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 168. 1895; Jepson, Man. Fl. Pl. Calif. 769. 1925.

Low, subsucculent, perennial herbs. Stems erect or more or less diffuse, terete; branches alternate or rather indefinitely clustered from the base. Leaves opposite, petiolate, the blade rather thick and subsucculent, entire, penninerved, eglandular; petioles winged and concrescent at the nodes, exappendiculate. Inflorescence rather irregularly dichasial, lateral or pseudoterminal, the pedicels subtended by solitary bracts. Flowers showy, reddish-violet or nearly cream-colored. Calyx 5-parted, the lobes subequal, imbricated, cleft nearly to the receptacle, eglandular. Corolla infundibuliform, the tube straight, greatly inflated at the insertion of the stamens into a conical throat, the limb 5-parted, actinomorphic, dextrorsely convolute. Stamens 5, inserted at the base of the corollathroat, wholly included; anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, sagittate, narrowly 2-auriculate connective; pollen granular; filament short, ligular, minutely pilose. Carpels 2, united at the apex by an elongate, stylar shaft surmounted by the subcapitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectary annular, completely concrescent. Follicles apocarpous or occasionally united at the tips, terete, relatively stout, falcate, dehiscing along the ventral suture, containing many dry, compressed, apically comose seeds; embryo straight, the cotyledons ovate, concave.

Type species: *Cycladenia humilis* Benth. Pl. Hartw. 322. 1849.

1. *Cycladenia humilis* Benth. Pl. Hartw. 322. 1849; A. Gray, Syn. Fl. N. Am. ed. 1. 2<sup>1</sup>: 83. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 168. 1895; Jepson, Man. Fl. Pl. Calif. 769. 1925.

Low, subsucculent, perennial herbs from a stout tap-root; stems 1–2 dm. tall; leaves opposite, petiolate, the blade rather thick, ovate to suborbicular, apex obtuse to rounded, base obtuse to obscurely cordate, rather gradually produced into the petiole, 3–7 cm. long, 2–6 cm. broad, greatly reduced below, the petiole 0.5–3.0 cm. long; cymes few- to several-flowered, about equalling or somewhat surpassing the subtending leaves; pedicels 0.75–1.25 cm. long, the subtending bracts narrowly lanceolate, 0.2–0.5 cm. long; calyx-lobes ovate-lanceolate to linear, acuminate, 0.5–0.75 cm. long; corolla showy, reddish-violet to cream-colored, the proper-tube 0.25–0.5 cm. long, about 0.2 cm. in diameter at the base, the throat conical, 0.5–0.75 cm. long, about 0.4–0.6 cm. in diameter at the orifice, the lobes obovate-oblong, 0.5–0.75 cm. long, spreading; anthers 0.35 cm. long, minutely papillate dorsally; ovary ovoid, rather abruptly produced into the style, about 0.15 cm. long; nectary annular, about half as high as the ovary; stigma subcapitate, 0.1 cm. long; follicles relatively stout, essentially continuous, falcate or slightly divaricate, 3.5–7.0 cm. long, about 0.3–0.5 cm. in diameter; seeds 0.75 cm. long, the pale tawny coma 1.5–2.0 cm. long.

### Var. *typica*.

Plants glabrous and glaucous throughout.

UNITED STATES: CALIFORNIA: edge of lavas, Medicine Peak, Siskiyou Co., alt. 6000 ft., Aug. 5, 1893, *Baker s.n.* (UC); Sisson, Siskiyou Co., lower Canadian zone, July 16, 1902, *Setchell & Dobie s.n.* (UC); Snow Mt., Lake Co., alt. 7800 ft., Aug., 1894, *Purpus 851* (UC); Cobb Mt., Lake Co., July, 1893, *Leithold s.n.* (UC, LS); high slopes, Greenville and Lassen Lake, Plumas Co., July, 1872, *Lemmon 119* (UC); Lassen's Peak, Lassen Co., Aug., 1896, *Austin s.n.* (MBG); Sierra Co., 1875, *Lemmon 187* (MBG); peaks of Plumas Co., June, year lacking, *Lemmon s.n.* (MBG, UC); Greenville, Plumas Co., June 4, 1920, *Clemens s.n.* (CA); Mt. Lassen, Lassen Co., July 10, 1923, *Bassett s.n.* (CA); Lassen Volcanic Park, Lassen Co., June, 1927, *Sutcliffe s.n.* (CA); southeast side of Snow Mt. above Bonnie View, Lake Co., June 7, 1919, *Heller 13229* (CA, LS, MBG); Cedar Glen, Sierra Co., May 25, 1920, *V. Jones s.n.* (CA); Prospect Peak, 1929, *Kramer s.n.* (CA); Cobb Mt., near top,



alt. 4000 ft., May 31, 1927, *Baker 2180A* (LS); Lassen's Peak, Lassen Co., alt. 6000 ft., July 8, 1897, *M. E. Jones s.n.* (LS, PC); mesa near Black Butte, Siskiyou Co., Aug. 9, 1899, *Dudley s.n.* (LS); Silver Lake, Lassen Co., July 30, 1894, *Baker s.n.* (LS, UC); top of ridge west of Camp, Sta. Lucia Mts., Aug. 11, 1903, *Dudley s.n.* (LS); Indian Valley, June 2, 1873, *Lenmon s.n.* (LS); Mt. Bailey, Shasta Co., Sept. 26-28, 1862, *Brewer 1448* (UC); Dutch Hill, Butte Co., 1879, *Austin 370* (UC); Doe Mill, Butte Co., May, 1898, *Austin & Bruce 2422* (PC); data incomplete, *Hartweg s.n.* (Camb.).

**Var. *venusta*** (Eastw.) Woodson, in Munz, Man. So. Calif. Bot. 379. 1935.

*Cycladenia venusta* Eastw. Bull. Torrey Bot. Club 29: 77. 1902.

Calyx and corolla-tube conspicuously pilose; in all other essential characters similar to the typical variety.

UNITED STATES: CALIFORNIA: Summit, San Antonio Mt., Los Angeles Co., June, 1899, *Hall s.n.* (LS); same locality, alt. 3170 m., June, 1897, *Hasse s.n.* (LS); Mt. San Antonio, San Bernardino Co., July, 1901, *Abrams 1920* (LS, PC); south slope of Baldy, San Antonio Mts., dry ground under pines, alt. 7500 ft., July 4, 1917, *Johnston 1428* (LS, UC, PC); Cucamonga Peak, San Antonio Mts., sunny exposure, well-packed granitic soil, alt. 8200 ft., July 31, 1917, *Johnston 1550* (LS, UC, PC); Devil's Backbone, San Antonio Mts., dry rocky ground, alt. 9000 ft., July 4, 1917, *Johnston 1431* (LS, UC, PC); dry soil on Mt. San Antonio, alt. 8000 ft., July 16, 1893, *McClatchie s.n.* (LS); upper San Antonio Canyon, San Bernardino Co., July 8, 1926, *M. E. Jones s.n.* (LS); Santa Lucia Mts., date lacking, *Abbott s.n.* (CA); Santa Lucia Peak, Oct. 3, 1921, *Clemens s.n.* (CA); Santa Lucia Mts., June 9, 1893, *Eastwood s.n.* (UC); southern slope of Mt. San Antonio, San Gabriel Mts., Los Angeles Co., on open talus slopes, alt. 10,000 ft., July 28-30, 1930, *Goodman & Hitchcock 1720* (MBG); gravelly ridges near summit, San Antonio Mt., alt. 9500 ft., June, 1899, *Hall 1231* (UC); San Antonio Mt., alt. 8000 ft., Aug. 20, 1905, *Wilder 591* (UC); ridge east of Ontario Peak, San Gabriel Mts., occasional on dry ridge, alt. 8300 ft., July 18, 1922, *Munz 6094* (PC); UTAH: San Rafael Swell, May 19, 1914, *M. E. Jones s.n.* (MBG, LS).

**Var. *tomentosa*** A. Gray, Syn. Fl. N. Am. ed. 2. 2<sup>1</sup>: 400. 1886.

*Cycladenia tomentosa* A. Gray, in Bot. Calif. Geol. Surv. 1: 474. 1876.

*Cycladenia humilis* Benth. var. *tomentosa* Jepson, Man. Fl. Pl. Calif. 769. 1925, in err.

Plants densely tomentose throughout; in all other essential characters similar to the typical variety with which it is occasionally found.

UNITED STATES: CALIFORNIA: Cedar Glen, Sierra Co., May 25, 1920, *V. Jones s.n.* (CA); Mt. Dyer, 1883, *Austin s.n.* (CA); Mt. Shasta, June, 1887, *Brandegge s.n.*

(MBG); Black Cone, near Shasta, date lacking, *Lemmon s.n.* (MBG, G, TYPE, UC, LS); Dutch Hill, Butte Co., 1879, *Austin 376* (UC); between Sisson's and Edgewood, Siskiyou Co., July, 1887, *Brandegge s.n.* (UC); trail between Indian Valley and Mountain Meadows, July, 1872, *Lemmon s.n.* (UC); mesa, near Black Butte, Siskiyou Co., Aug. 9, 1899, *Dudley s.n.* (LS).

Although its relatively isolated geographical distribution might appear to argue its specificity, *C. venusta* Eastw. has been reduced to varietal rank since it has no distinctive characteristic except its relatively restricted indument.

## XX. ECHITES P. Br.

**Echites** P. Br. Hist. Jam. 2: 182. 1756; Jacq. Enum. Pl. Carib. 13. 1760, in part; Select. Stirp. Am. Hist. 1: 30. 1763; L. Sp. Pl. ed. 2. 307. 1762; Gen. Pl. ed. 6. 117. 1764; A. DC. in DC. Prodr. 8: 446. 1844; Miers, Apoc. So. Am. 191. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 165. 1895, all in part, as to *E. umbellata* Jacq.

Lactescent, suffruticose or suffrutescent lianas. Stems voluble, terete; branches usually opposite below, becoming alternate above. Leaves opposite, petiolate, entire, penninerved, eglandular; petioles somewhat girdling at the node into an inconspicuous, minutely appendiculate, stipular ring. Inflorescence lateral, or rarely subterminal or terminal, alternate, a more or less modified dichasium, bracteate, bearing solitary to numerous flowers. Calyx 5-parted, the lobes equal or subequal, cleft nearly to the receptacle, bearing within at the base a solitary, frequently deeply dissected, opposite squamella. Corolla salverform, the tube straight, exappendiculate, not annulate, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers wholly included, connivent and agglutinated to the stigma, consisting of 2 parallel sporangia with a conspicuous, protuberant base borne ventrally near the apex of an enlarged, sagittate, narrowly 2-auriculate connective; pollen granular. Carpels 2, apocarpous, united at the apex by an elongate, stylar shaft surmounted by the fusiform-subcapitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or more

or less conerescent. Follicles 2, apocarpous, terete, continuous or only slightly articulated, dehiscing along the ventral suture, containing many dry, rostrate, apically comose seeds.

Type species: *Echites umbellata* Jacq. Enum. Pl. Carib. 13. 1760.

#### KEY TO THE SUBGENERA AND SECTIONS

- A. Corolla 1.25–2.5 cm. long, the lobes narrowly oblong- to elliptic-lanceolate, reflexed at anthesis; inflorescence relatively lax and many-flowered....  
.....Subgen. I. PSEUDECHITES
- AA. Corolla 5–8 cm. long, the lobes obliquely obovate, spreading at anthesis; inflorescence relatively compact, few- to several-flowered  
.....Subgen. II. EUECHITES
- B. Corolla-tube not spirally contorted; species of Central America.....  
.....Sect. 1. YUCATANENSES
- BB. Corolla-tube spirally contorted; plants of southern peninsular Florida, the Bahama Islands, the Antilles, and locally of the peninsula of Yucatan and Atlantic coastal Colombia.....Sect. 2. UMBELLATAE

Subgen. I. PSEUDECHITES Woodson, subgen. nov.

Corolla 1.25–2.5 cm. long, the lobes narrowly oblong- to elliptic-lanceolate, long-acuminate, reflexed at anthesis; inflorescence relatively lax and several- to many-flowered. *Spp.* 1–2.

#### KEY TO THE SPECIES

- a. Corolla 1.25–1.8 cm. long, the lobes somewhat shorter than the tube; ovary and nectaries glabrous.....1. *E. tuxtlensis*
- aa. Corolla 2.0–2.5 cm. long, the lobes about twice surpassing the tube; ovary puberulent-papillate, nectaries minutely pilosulose-barbate....3. *E. turbinata*

1. ***Echites tuxtlensis*** Standl. Contr. U. S. Nat. Herb. 23: 1164. 1924.

Stems relatively slender, glabrous; leaves opposite, shortly petiolate, narrowly lanceolate- to obovate-elliptic, apex acuminate, base cuneate, 6–10 cm. long, 1.5–3.5 cm. broad, firmly membranaceous to subcoriaceous, glabrous; petioles 0.3–0.8 cm. long; inflorescence lateral, alternate, a lax, dichotomous, bostrychoid dichasium bearing several to many small, yellowish-green flowers, much surpassing the subtending leaves, wholly glabrous; pedicels 0.7–1.0 cm. long; bracts minutely trigonal, about 0.1 cm. long, or somewhat less; calyx-lobes ovate-trigonal, acute to acuminate, 0.1–0.15 cm. long, glabrous, the squamellae deltoid, minutely erose; corolla salverform,

glabrous without, the tube 0.8–1.0 cm. long, about 0.1 cm. in diameter at the base, slightly dilating somewhat above the base at the insertion of the stamens, thence slightly constricting toward the orifice, the lobes oblong- to elliptic-lanceolate, acuminate, somewhat shorter than the tube, more or less reflexed at anthesis; stamens inserted near the base of the corolla-tube, the anthers narrowly elliptic-sagittate, 0.55 cm. long, glabrous; ovary oblong-ovoid, about 0.1 cm. long, glabrous; stigma 0.1 cm. long; nectaries separate, about half equalling the ovary; follicles known.

MEXICO: CHIAPAS: near Tuxtla, alt. 2400–2800 ft., Sept. 1, 1895, *Nelson 3080* (US, TYPE, MBG, photograph and analytical drawings).

BRITISH HONDURAS: high ridge, Corozal District, 1931–32, *Gentle 439* (MBG); Maskall, Northern River, Dec., 1933, *Gentle 1022* (MBG).

COSTA RICA: Heredia, in Monte Barba, date lacking, *Ørsted 15544* (C).

**2. *Echites turbinata* Woodson, Ann. Mo. Bot. Gard. 21: 615. 1934.**

Stems relatively stout, glabrous; leaves opposite, petiolate, elliptic, apex acuminate, base broadly obtuse, 7.5–12.0 cm. long, 3.5–7.0 cm. broad, firmly membranaceous, evidently somewhat subsucculent, glabrous; petioles 0.8–1.3 cm. long; inflorescence lateral, alternate, rather irregularly dichasial, about equalling the subtending leaves, bearing several rather small, yellowish-green (?) flowers, glabrous throughout; pedicels 0.8–1.0 cm. long; bracts ovate-lanceolate, 0.13–0.3 cm. long; calyx-lobes ovate, acuminate, 0.3–0.32 cm. long, glabrous, the squamellae deltoid, minutely denticulate; corolla salverform, minutely puberulent-papillate without, the tube 0.7–0.8 cm. long, about 0.15 cm. in diameter at the base, slightly constricting toward the orifice, the lobes narrowly elliptic-lanceolate, acuminate, 1.4–1.6 cm. long, somewhat turbinate; stamens inserted about midway within the corolla-tube, the anthers rather narrowly trigonal-sagittate, 0.45 cm. long, glabrous; ovary ovoid, very minutely puberulent-papillate, about 0.15 cm. long; stigma 0.15 cm. long; nectaries separate, somewhat shorter than the ovary, minutely pilosulose-barbate at the tips; follicles unknown.

COSTA RICA: forets du Rancho Flores, Febr. 22, 1890, *Tondus 2147* (B, TYPE, MBG, photograph and analytical drawings).

A drawing of the inflorescence of this species, with remarks on its structure, will be found in *Ann. Mo. Bot. Gard.* 22: 14. *pl. 2, fig. 2.* 1935.

Subgen. II. *EUECHITES* Woodson, subgen. nov.

Corolla 5–8 cm. long, the lobes obliquely obovate, obtuse to shortly acuminate, spreading at anthesis; inflorescence relatively compact, few- to several-flowered. *Sects. 1–2.*

Sect. 1. *YUCATANENSES* Woodson. Corolla relatively delicate in texture, the buds attenuate, the tube straight, not spirally contorted. Species of Central America. *Spp. 3–5.*

#### KEY TO THE SPECIES

- a. Inflorescence almost perfectly dichasial to simply helicoid, not subumbellate.....3. *E. turrigera*
- aa. Inflorescence subumbellate.
  - b. Leaves coriaceous or subcoriaceous, more or less pandurate, conspicuously nitidulous above with verrucose venation.....4. *E. yucatanensis*
  - bb. Leaves rather delicately membranaceous, evidently never pandurate, opaque above, the venation not verrucose.....5. *E. elegantula*

3. *Echites turrigera* Woodson, *Ann. Mo. Bot. Gard.* 19: 381. 1932.

*Echites cincinnalis* Woodson, loc. cit. 21: 616. 1934.

Stems relatively slender, rather inconspicuously pilosulose when young, eventually becoming glabrate; leaves opposite, petiolate, broadly oblong- to ovate- or obovate-elliptic, apex rather shortly acuminate, base obtuse to rounded, rarely obscurely cordate, 5–15 cm. long, 3–10 cm. broad, membranaceous, wholly glabrous, somewhat nitidulous and the venation somewhat verrucose above, rather pale yellowish-green; petioles 0.8–4.0 cm. long, glabrous; inflorescence lateral to subterminal, alternate, almost perfectly dichasial to simply helicoid, somewhat surpassing the subtending leaves, bearing 6–20 rather showy, white or cream-colored flowers; peduncle minutely pilosulose-scabridulous to glabrate; pedicels 1.0–1.2 cm. long, minutely pilosulose-scabridulous to nearly glabrate; bracts oblong-lanceolate, acuminate, somewhat foliaceous, 0.1–0.3 cm.

long; calyx-lobes lanceolate, acuminate, 0.3–0.7 cm. long, rather sparsely pilosulose, the squamellae erose to lacerate; corolla salverform, glabrous without, the tube 2.8–3.8 cm. long, about 0.15–0.2 cm. in diameter at the base, rather conspicuously and abruptly dilated somewhat below midway at the insertion of the stamens, thence rather gradually constricting toward the orifice, the lobes obliquely obovate, shortly acuminate, 1.5–2.0 cm. long, spreading; anthers rather narrowly oblong-sagittate, 0.75–0.8 cm. long, glabrous; ovary oblongoid, about 0.15–0.2 cm. long, glabrous; stigma 0.15 cm. long; nectaries separate or rather indefinitely concrescent, somewhat less than half equaling the ovary; immature follicles rather sparsely pilosulose.

GUATEMALA: ZACAPA: Gualan, alt. 620 ft., June 20, 1909, *Deam 6376* (MBG, TYPE, NY); JUTIAPA: Laguna de Guija, alt. 1200 m., April, 1894, *Heyde & Lux 6345* (NY).

NICARAGUA: GRANADA: environs de Granada, alt. 40 m., autumn, 1869, *Lévy 1074* (C, MBG, photograph and analytical drawings); low hills near Granada, edge of thicket, July 2, 1923, *Maxon Harvey & Valentine 7614* (US).

When *E. cincinnalis* was originally described, only two of the specimens cited above were known to me, *Lévy 1074*, the type of *E. cincinnalis*, and *Deam 6376*, the type of *E. turrigera*. The former species was erected upon the basis of a simple, cincinnal inflorescence, that of *E. turrigera* being an almost perfect, compound dichasium. Geographical distribution was also a fancied support for the distinction of the species. However, with the examination of *Heyde & Lux 6345* and *Maxon Harvey & Valentine 7614*, it appears probable that the inflorescence of the collective species is much more variable than is usual, and it has been decided to consolidate the two former species, at least until additional evidence warranting their segregation is forthcoming.

**4. *Echites yucatanensis* Millsp. ex Standl.** Field Mus. Publ. Bot. 8: 35. 1930.

Stems relatively stout, glabrous; leaves opposite, ovate to oblong, frequently irregularly pandurate, apex acuminate, base obtuse to rounded, 7–12 cm. long, 2.5–7.0 cm. broad, coriaceous to subcoriaceous, dark green and nitidulous above, the venation

conspicuously verrucose, opaque beneath, glabrous throughout; petioles 1–2 cm. long; inflorescence lateral, alternate, subumbellate, bearing 3–9 greenish-yellow (?) flowers; peduncle glabrous, usually somewhat shorter than the subtending leaves; pedicels 1.0–1.3 cm. long, glabrous; bracts ovate-lanceolate, minute, scarious; calyx-lobes ovate-lanceolate, acuminate, 0.18–0.2 cm. long, glabrous, the squamellae deltoid, minutely erose; corolla salverform, glabrous without, the tube 4.0–4.5 cm. long, about 0.2 cm. in diameter at the base, somewhat below midway abruptly dilated at the insertion of the stamens, thence gradually constricting toward the orifice, the lobes obliquely obovate, shortly acuminate, 2.5–3.0 cm. long, spreading; anthers lanceolate-sagittate, 1.0–1.2 cm. long, glabrous; ovary oblongoid, about 0.15 cm. long, glabrous; stigma 0.2 cm. long; nectaries more or less concrescent at the base, less than half equalling the ovary; follicles relatively slender, acuminate, continuous, rigidly divaricate, 16–25 cm. long, glabrous; seeds 1.0–1.2 cm. long, the tawny coma 1.5–2.0 cm. long.

MEXICO: CAMPECHE: small vine, Tuxpeña, Febr. 18, 1932, *Lundell 1350* (MBG, NY, US); YUCATAN: Chichankanab, date lacking, *Gaumer 1979* (C, MBG, S, isotypes); in clearing, Chichen-Itza, June 22, 1932, *Steere 1471* (MBG); Xkantunil, date lacking, *Gaumer 817* (S); Izamal, date lacking, *Gaumer 817* (C).

**5. *Echites elegantula* Woodson, Am. Jour. Bot. 22: 686. 1935.**

Stems relatively slender, glabrous; leaves opposite, shortly petiolate, ovate-elliptic, apex acutely subcaudate-acuminate, base obtuse and somewhat decurrent, 5–8 cm. long, 2.0–3.5 cm. broad, rather delicately membranaceous, opaque, glabrous, the veins not verrucose above; petioles 0.5–1.0 cm. long; inflorescence lateral, alternate, subumbellate, bearing 4–8 showy, greenish cream-colored flowers; peduncle about half equalling the subtending leaves, essentially glabrous; pedicels 1.5–2.0 cm. long, glabrous; bracts linear, 0.2–0.3 cm. long; calyx-lobes lanceolate, acuminate, 0.3–0.5 cm. long, indistinctly papillate without, the squamellae subquadrate, essentially entire; corolla salverform, very minutely papillate without, the tube 5.0–5.5 cm. long, about 0.15 cm. in diameter at the base, some-

what below midway abruptly dilated at the insertion of the stamens, thence gradually constricting toward the orifice, the lobes obliquely obovate, obtuse, 3.0–3.5 cm. long, spreading; anthers elliptic-lanceolate, obtusely auriculate, 0.9 cm. long, glabrous; ovary oblongoid, about 0.3 cm. long, glabrous; stigma 0.3 cm. long; nectaries concrescent, somewhat less than half equalling the ovary; follicles unknown.

MEXICO: YUCATAN: over tree in forest, Chichen-Itza, June 23, 1932, *Steere 1477* (MBG, TYPE).

The obtusely auricled anthers are an exception to the general rule of this genus.

Sect. 2. *UMBELLATAE* Woodson. Corolla relatively fleshy in texture, the buds obtuse, the tube spirally contorted. Plants of southern peninsular Florida, the Bahama Islands, the Antilles, and locally of the peninsula of Yucatan and Atlantic coastal Colombia. *Sp. 6.*

#### 6. *Echites umbellata* Jacq.

Stems relatively stout, glabrous; leaves opposite, shortly petiolate, narrowly oblong-elliptic to suborbicular, apex acuminate to rounded and somewhat retuse, base obtuse to rounded, occasionally somewhat cordate, firmly membranaceous or somewhat subsucculent, glabrous; inflorescence lateral to subterminal, alternate, irregularly dichasial to subumbellate, glabrous throughout; peduncle somewhat shorter than the subtending leaves, or virtually lacking, bearing relatively few greenish-yellow flowers; pedicels 1.0–1.5 cm. long, glabrous, greatly accrescent in fruit; bracts ovate to ovate-lanceolate, 0.15–0.3 cm. long, only slightly foliaceous; calyx-lobes ovate to narrowly oblong-trigonal, acute to acuminate, 0.15–0.5 cm. long, glabrous, scarious or only slightly foliaceous, the squamellae very deeply lacerate; corolla salverform, glabrous without, 2.0–5.5 cm. long, about 0.15–0.2 cm. in diameter at the base, somewhat dilated slightly below midway at the insertion of the stamens, thence gradually constricting toward the orifice, spirally contorted above the insertion of the stamens, the lobes



obliquely obovate, obtuse to very inconspicuously apiculate, 1.1–3.0 cm. long, spreading; stamens inserted slightly below midway within the corolla-tube, the anthers narrowly lanceolate-sagittate, 0.9–1.2 cm. long, glabrous; ovary oblongoid, about 0.15 cm. long, glabrous; stigma 0.2 cm. long; nectaries essentially separate, about equalling to about half equalling the ovary; follicles relatively stout, continuous, acuminate, rigidly divaricate, 9–26 cm. long, glabrous; seeds 0.5–0.85 cm. long, the tawny coma 1.5–5.0 cm. long.

**Var. typica.**

*Echites umbellata* Jacq. Enum. Pl. Carib. 13. 1760; Select. Stirp. Am. Hist. 1: 30; 2: pl. 22. 1763; A. DC. in DC. Prodr. 8: 447. 1844; Miers, Apoc. So. Am. 193. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 165. 1895.

*Tabernaemontana Echites* L. Syst. Pl. ed. 10. 945. 1759.

*Echites litorea* HBK. Nov. Gen. 3: 212. 1819; A. DC. loc. cit. 448. 1844; Miers, loc. cit. 199. 1878.

*Echites umbellata* Jacq. var. *longiflora* Griseb. Cat. Pl. Cub. 172. 1866.

*Echites ovata* P. Br. ex Miers, loc. cit. 192. 1878, in err.

*Echites obliqua* Miers, loc. cit. 193. 1878.

*Echites longiflora* (Griseb.) Miers, loc. cit. 194. 1878.

*Echites Echites* (L.) Britton, in Small, Fl. Miami, 147. 1913.

Leaves narrowly oblong-elliptic to suborbicular, 4–12 cm. long, 2.0–7.6 cm. broad; petioles 0.3–1.5 cm. long; inflorescence 2–7-flowered, the peduncle manifest, somewhat shorter than the subtending leaves.

UNITED STATES: FLORIDA: sandy field at Cape Sable, July, year lacking, *Curtiss 2266* (MBG, NY, US); climbing over bushes, Old Rhodes Key, July 2, 1895, *Curtiss 5448* (MBG, NY, US); Miami, May 7, 1904, *Tracy 9185* (MBG, NY); pinelands between Miami and Kendall Station, Nov. 5, 1906, *Small & Carter 2657* (NY); Key West, 1874, *Palmer 438* (MBG); on dunes, uncommon here, Palm Beach, June 7, 1896, *Webber 434* (MBG); pinelands, Big Pine Key, Febr. 27, 1911, *Small Carter & Small 3545* (NY); pinelands between Peter's Prairie and Homestead, Nov. 10, 1906, *Small & Carter 2655* (NY); pinelands about Cox Hammock, Dade Co., June

24, 1915, *Small Mosier & Small 6582* (NY); Snapper Creek, south of Coconut Grove, Oct. 27–31, 1901, *Small & Nash s.n.* (NY).

BAHAMA ISLANDS: The Bight and vicinity, Cat, March 1–6, 1907, *Britton & Millspaugh 5887* (NY); Governor's Harbor, Nov. 14, 1890, *Hitchcock 16* (MBG); Abraham Bay and vicinity, Mariguana, Dec. 6–8, 1907, *Wilson 7458* (NY); Eleuthera Bluff, Eleuthera, Jan. 10, 1932, *Fairchild s.n.* (US); Water Key, Salt Key Bank, May 22, 1909, *Wilson 8148* (MBG, NY); southeast end, Watling's, Nov. 27–28, 1907, *Wilson 7273* (NY); Grand Turk, Aug. 27–Sept. 1, 1905, *Nash & Taylor 3890* (NY); coppice, Green Turtle Cay, Abaco, Dec. 4, 1904, *Brace 1492* (NY); west end, Great Bahama, April 16–May 8, 1905, *Brace 3588* (NY); vicinity of Blue Hills, New Providence, May 28–29, 1909, *Wilson 8240* (NY); Mangrove Cay, Andros, Aug. 18–Sept. 10, 1906, *Brace 4397* (MBG); South Caicos, Dec. 14–16, 1907, *Wilson 7595* (MBG, NY); Gold Rock, Acklin's, Dec. 21, 1905–Jan. 6, 1906, *Brace 4399* (NY, US).

CUBA: PINAR DEL RIO: palm-barrens west of Guane, Nov. 21–22, 1911, *Shafer 10370* (MBG, NY, US); limestone hills, vicinity of Sumiduro, July 28–31, 1912, *Shafer 13419* (NY, US); ISLA DE PINOS: over bushes on river bank, near Nueva Gerona, July 8, 1900, *Palmer & Riley 1041* (US); HABANA: near Morro Castle, May 20, 1908, *Leon 713* (NY); climbing through bushes in swamp near the sea, Playa de Marianao, June 17, 1900, *Palmer & Riley 842* (US); MATANZAS: coral rock soil east of Matanzas, March 13, 1903, *Britton Britton & Shafer 176* (NY); Playa, Aug. 28, 1903, *Britton & Wilson 59* (NY); SANTA CLARA: Cienegueta, May 9, 1895, *Combs 17* (MBG); dry field, vicinity of Sancti Spiritus, Febr. 15–24, 1912, *Shafer 12167* (NY); CAMAGUEY: Cayo Paloma, Oct. 12, 1909, *Shafer 2590* (MBG, NY, US); vicinity of La Gloria, Febr. 4, 1909, *Shafer 302* (NY, US); ORIENTE: Cave Hill, limestone hills, south of Holguin, April 11, 1909, *Shafer 1236* (NY, US); Punta Maisi, Dec. 14, 1910, *Shafer 7930* (NY).

JAMAICA: climbing over shrubs, Constant Spring to Bardowie, Febr. 8, 1915, *Harris 12109* (MBG, NY, US); in sand, coastal region east of Montego Bay, sea-level, March 28, 1920, *Maxon & Killip 1615* (US); Port Royal, Dec. 18, 1890, *Hitchcock s.n.* (MBG); Bog Walk, Dec. 17, 1890, *Hitchcock s.n.* (MBG).

HISPANIOLA: SANTO DOMINGO: Paradis, prope Barahona, in fruticetis litoralibus, Dec., 1909, *Tuerckheim 2689* (NY, US); southeast of town, San Pedro de Macoris, March 31, 1913, *Rose Fitch & Russell 4292* (NY, US); semi-arid pine region, Moncion, Prov. Monte Cristy, alt. 375 m., June 5, 1930, *Valeur 444* (MBG, US); Lajana, Samana Peninsula, alt. about 100 m., Apr. 30–May 2, 1922, *Abbott 2275* (US); HAITI: twining on shrubs, bluff east of Bord de Mer, vicinity of Jean Rabel, Jan. 27–Febr. 9, 1929, *Leonard & Leonard 12883* (NY, US); downs of cliff-bordered shore west of Cabaret, Baie des Moustiques, Jan. 13, 1929, *Leonard & Leonard 11923* (US); thickets on coral rocks east of La Tete Linne, vicinity of Basse Tierce, Tortue Island, March 24, 1929, *Leonard & Leonard 14070* (US); a common vine, Miragoane and vicinity, April 12, 1927, *Eyerdam 431* (US); hillside, Bayeux, near Port Margot, Aug. 4, 1903, *Nash 138* (NY, US).

MEXICO: YUCATAN: Isla Mujeres, March 24–26, 1901, *Goldman 646* (US); in clearing, Uxmal, July 20–21, 1932, *Steere 1987* (MBG).

BRITISH HONDURAS: coastal region, Honey Camp, Sept., 1929, *Lundell 515* (MBG, NY, US).

COLOMBIA: San Andres Island, June, 1929, *Toro 28* (NY).

Var. **crassipes** (A. Rich.) Gomez, Anal. Soc. Espan. Hist. Nat. 23: 274. 1894.

*Echites crassipes* A. Rich. in Sagra, Hist. Cuba 11: 91. 1850.

*Rhodocalyx crassipes* (A. Rich.) Miers, Apoc. So. Am. 140. 1878.

Leaves narrowly oblong-elliptic to nearly linear, 1–6 cm. long, 0.2–1.5 cm. broad; petioles 0.1–0.3 cm. long; peduncle obsolete or scarcely manifest, the solitary pedicels apparently sessile.

CUBA: HABANA: Cuabal de Jesus Maria, Minas, June 24, 1915, *Leon 5211* (NY); MATANZAS: serpentine hills near Canasi, Oct. 10, 1927, *Leon 13138* (NY); SANTA CLARA: on bushes, Sagua, Sept. 4, 1903, *Britton & Wilson 327* (NY); CAMAGUEY: Santayana, in palm barrens in serpentine, Oct. 4, 1922, *Ekman 1533* (S); ORIENTE: Holguin, Cerro de Fraile, in fruticetis, Sept. 25, 1916, *Ekman 7549* (S); barren savannas, southeast of Holguin, rocky places, Nov. 26–29, 1909, *Shafer 2951* (NY).

These plants appear to be no more than microphyllous, depauperate individuals of var. *typica*, and it is doubtful whether they should even be recognized as a variety. The reduction of the primary peduncle is perhaps their greatest distinction.

#### EXCLUDED OR UNCERTAIN SPECIES

*Echites acuminata* R. & P. Fl. Peruv. 2: 19. pl. 134. 1799 = **Mesechites acuminata** (R. & P.) Muell.-Arg. Linnaea 30: 446. 1860.

*Echites acutiloba* A. DC. in DC. Prodr. 8: 451. 1844 = **Mandevilla acutiloba** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 54. 1932.

*Echites adglutinata* Jacq. Select. Stirp. Am. Hist. 1: 31; 2: pl. 23. 1763, err. typ. = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760 = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites albiflora* Miers, Apoc. So. Am. 204. 1878 = **Tabernaemontana** sp. The present taxonomic confusion of the genus

*Tabernaemontana* precludes a precise relegation of this synonym.

*Echites alexicaca* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 68. 1841 = **Mandevilla illustris** (Vell.) Woodson var. **glabra** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 20: 729. 1933 (*Dipladenia illustris* (Vell.) Muell.-Arg.  $\beta$  **glabra** Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 125. pl. 38. 1860).

*Echites almadensis* Stadelm. Flora 24<sup>1</sup>: Beibl. 28. 1841 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792, not R. & P.).

*Echites altescandens* H. Winkl. in Fedde, Rep. Spec. Nov. 7: 243. 1909 = **Mandevilla antennacea** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites antennacea* A. DC. in DC. Prodr. 8: 456. 1844).

*Echites amazonica* Stadelm. Flora 24<sup>1</sup>: Beibl. 50. 1841 = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932 (*Echites verrucosa* R. & S. Syst. 4: 795. 1819).

*Echites andina* (Muell.-Arg.) Miers, Apoc. So. Am. 204. 1878 (*Amblyanthera andina* Muell.-Arg. Linnaea 30: 425. 1860) = **Mandevilla riparia** (HBK.) Woodson, Ann. Mo. Bot. Gard. 19: 58. 1932 (*Echites riparia* HBK. Nov. Gen. 3: 214. 1819).

*Echites Andrewsii* Chapm. Fl. So. U. S. 359. 1860 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites Andrieuxii* (Muell.-Arg.) Miers, Apoc. So. Am. 206. 1878 (*Amblyanthera Andrieuxii* Muell.-Arg. Linnaea 30: 422. 1860) = **Mandevilla Andrieuxii** (Muell.-Arg.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Echites angustifolia* Benth. in Hook. Jour. Bot. 3: 247. 1841, not Poir. = **Mandevilla Benthamii** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites Benthamii* A. DC. in DC. Prodr. 8: 467. 1844).

*Echites angustifolia* Poir. Encycl. Suppl. 2: 537. 1812 = **Mesechites angustifolia** (Poir.) Miers, Apoc. So. Am. 230. 1878.

*Echites annularis* L. f. Suppl. 166. 1781 = **Prestonia annularis** (L. f.) G. Don, Gen. Hist. 4: 84. 1838.

*Echites antennacea* A. DC. in DC. Prodr. 8: 456. 1844 = **Mandevilla antennacea** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites* (*Amblyanthera* ?) *apocynifolia* A. Gray, Proc. Am. Acad. 22: 435. 1887 = **Mandevilla apocynifolia** (A. Gray) Woodson, Ann. Mo. Bot. Gard. 19: 65. 1932.

*Echites arborea* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 47. 1827 = **Malouetia arborea** (Vell.) Miers, Apoc. So. Am. 89. 1878.

*Echites aspera* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 359. 1844. This may possibly refer to *Mandevilla subsagittata* (R. & P.) Woodson. The type specimen, *Galeotti 1587*, was unavailable during these studies although special search was made for it in the principle collections of Europe and America.

*Echites asperuginis* Sw. Prodr. 52. 1788 = **Anechites lapulacea** (Lam.) Miers, Apoc. So. Am. 237. 1878 (*Echites lapulacea* Lam. Encycl. 2: 341. 1786).

*Echites assimilis* K. Sch. in Engl. Bot. Jahrb. 25: 724. 1898 = **Mandevilla riparia** (HBK.) Woodson, Ann. Mo. Bot. Gard. 19: 58. 1932 (*Echites riparia* HBK. Nov. Gen. 3: 214. 1819).

*Echites atropurpurea* Lindl. in Paxt. Mag. Bot. 9: 199. 1842 = **Mandevilla atrovioleacea** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 724. 1933 (*Echites atrovioleacea* Stadelm. Flora 24<sup>1</sup>: Beibl. 75. 1841).

*Echites atrovioleacea* Stadelm. Flora 24<sup>1</sup>: Beibl. 75. 1841 = **Mandevilla atrovioleacea** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 724. 1933.

*Echites augusta* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 48. 1827 = **Macrosiphonia longiflora** (Desf.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 140. pl. 43. 1860 (*Echites longiflora* Desf. Mem. Mus. Paris 5: 177. pl. 20. 1819).

*Echites auriculata* Pohl ex Stadelm. Flora 24<sup>1</sup>: Beibl. 25. 1841 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites axillaris* Sesse & Moc. Fl. Mex. 45. 1887. Description impossible to interpret.

*Echites Bangii* Rusby, Bull. N. Y. Bot. Gard. 4: 409. 1907 = **Prestonia acutifolia** (Benth.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895 (*Haemadictyon acutifolium* Benth. ex Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 167. 1860).

*Echites barbata* Desv. in Ham. Prodr. 30. 1788 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites barbata* Sesse & Moc. Fl. Mex. 45. 1887, non Desv. Description impossible to interpret.

*Echites Benthami* A. DC. in DC. Prodr. 8: 467. 1844 = **Mandevilla Benthami** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844 = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878.

*Echites bicolor* Miq. Stirp. Surinam. Select. 154. 1851 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites bicorniculata* Rusby, Descr. So. Am. Pl. 86. 1920 = **Mesechites bicorniculata** (Rusby) Woodson, Ann. Mo. Bot. Gard. 19: 387. 1932.

*Echites bicornis* Spruce, ex Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 114. 1860, nom. nud. in synonym. = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932 (*Echites verrucosa* R. & S. Syst. 4: 795. 1819).

*Echites biflora* Jacq. Enum. Pl. Carib. 13. 1760 = **Rhabdadenia biflora** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860.

*Echites bignoniaeflora* Schlecht. Linnaea 26: 372. 1853 = **Stemmadenia Galeottiana** (A. Rich.) Miers, Apoc. So. Am. 76. 1878 (*Odontostigma Galeottianum* A. Rich. in Sagra, Hist. Cuba 11: 87. pl. 56. 1850).

*Echites Billbergii* Beurl. Vet. Akad. Handl. Stockh. 137. 1854 (1856) = **Rhabdadenia biflora** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860 (*Echites biflora* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites Blanchetii* A. DC. in DC. Prodr. 8: 448. 1844 =

**Prestonia coalita** (Vell.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites coalita* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 40. 1827).

*Echites bogotensis* HBK. Nov. Gen. 3: 215. pl. 243. 1819 = **Mandevilla bogotensis** (HBK.) Woodson, Ann. Mo. Bot. Gard. 19: 73. 1932.

*Echites Boliriana* Britton, in Rusby, Mem. Torrey Bot. Club 4: 219. 1895 = **Mandevilla antennacea** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites antennacea* A. DC. in DC. Prodr. 8: 456. 1844).

*Echites brachyloba* (Muell.-Arg.) Miers, Apoc. So. Am. 203. 1878 = **Mandevilla brachyloba** (Muell.-Arg.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Amblyanthera brachyloba* Muell.-Arg. Linnaea 30: 423. 1860).

*Echites Brachysiphon* Torr. Bot. Mex. Bound. Surv. 158. 1859 = **Macrosiphonia Brachysiphon** (Torr.) A. Gray, Syn. Fl. N. Am. 2<sup>1</sup>: 83. 1878.

*Echites brachystachya* Benth. in Hook. Jour. Bot. 3: 248. 1841 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites bracteata* HBK. Nov. Gen. 3: 217. 1819 = **Mandevilla bracteata** (HBK.) O. Ktze. Rev. Gen. 2: 414. 1891.

*Echites bracteata* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 41. 1827, not HBK. or Mart. = **Forsteronia Velloziana** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 21: 622. 1934 (*Echites Velloziana* A. DC. in DC. Prodr. 8: 474. 1844).

*Echites bracteosa* Rusby, Mem. N. Y. Bot. Gard. 7: 325. 1927 = **Mandevilla bracteosa** (Rusby) Woodson, Ann. Mo. Bot. Gard. 20: 742. 1933.

*Echites breviflora* Urb. Symb. Ant. 5: 464. 1908 = **Mesechites angustifolia** (Poir.) Miers, Apoc. So. Am. 230. 1878 (*Echites angustifolia* Poir. Encycl. Suppl. 2: 537. 1812).

*Echites brevipes* Benth. Pl. Hartw. 216. 1845 = **Mesechites citrifolia** (HBK.) Woodson, Ann. Mo. Bot. Gard. 19: 387. 1932 (*Echites citrifolia* HBK. Nov. Gen. 3: 216. 1819).

*Echites Brownei* (A. DC.) Muell.-Arg. Linnaea 30: 446.

1860 (*Echites torosa* Jacq.  $\beta$  *Brownei* A. DC. in DC. Prodr. 8: 449. 1844) = **Mandevilla torosa** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 19: 64. 1932 (*Echites torosa* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites calycosa* A. Rich. in Sagra, Hist. Cuba 11: 94. 1850 = **Asketanthera calycosa** (A. Rich.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Echites campanulata* Sesse & Moc. Fl. Mex. 44. 1887. Description impossible to interpret.

*Echites campestris* Vell. Fl. Flum. 113. 1830; Icon. 3: pl. 43. 1827 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites canescens* Willd. ex R. & S. Syst. 4: 795. 1819 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites Catesbaei* G. Don, Gen. Hist. 4: 74. 1838 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Finca lutea* L. Cent. II. Pl. 12. 1756).

*Echites Chilensis* A. DC. in DC. Prodr. 8: 468. 1844 = **Elytropus chilensis** (A. DC.) Muell.-Arg. Linnaea 30: 140. 1860.

*Echites chlorantha* Schlecht. Linnaea 26: 663. 1853 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites Christophoriana* Ham. Prodr. 31. 1825. This may refer to *Mesechites repens* (Jacq.) Miers, as indicated by the description of small oval leaves, dichotomous lateral inflorescence, and small yellow flowers.

*Echites ciliata* Stadelm. Flora 24<sup>1</sup>: Beibl. 32. 1841 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites cinerea* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850 = **Haplophyton cinereum** (A. Rich.) Woodson, comb. nov. (*H. cimicidum* A. DC.). An unnumbered collection by Sagra bear-



ing the notation "*Echites cinerea*" is apparently the type specimen of this species. It is at present incorporated in the Natural History Museum at Vienna with the types of many others of Richard's Cuban species; and although the identity of the plant (represented in duplicate) is scarcely open to question, one can hardly avoid doubting the place of collection, as the genus *Haplophyton* is apparently limited in distribution to the semi-arid portions of northern Mexico and the southwestern United States.

*Echites circinalis* Sw. Prodr. 52. 1788 = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites citrifolia* HBK. Nov. Gen. 3: 216. 1819 = **Mesechites citrifolia** (HBK.) Woodson, Ann. Mo. Bot. Gard. 20: 637. 1933.

*Echites citrina* A. DC. in DC. Prodr. 8: 474. 1844 = **Marsdenia** sp. (perhaps closely related to *M. fusca* Wright).

*Echites coalita* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 40. 1827 = **Prestonia coalita** (Vell.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites Cobanensis* Donn. Sm. Bot. Gaz. 40: 6. 1905 = **Mandevilla tubiflora** (Mart. & Gal.) Woodson, Ann. Mo. Bot. Gard. 19: 52. 1932 (*Echites tubiflora* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 358. 1844).

*Echites coccinea* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834 = **Mandevilla coccinea** (Hook. & Arn.) Woodson, Ann. Mo. Bot. Gard. 20: 734. 1933.

*Echites cognata* Stadelm. Flora 24<sup>1</sup>: Beibl. 79. 1841 = **Odontadenia cognata** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 546. 1931.

*Echites comosa* O. Ktze. Rev. Gen. 2: 414. 1891 = **Mandevilla villosa** (Miers) Woodson, Ann. Mo. Bot. Gard. 19: 70. 1932 (*Laseguea villosa* Miers, Apoc. So. Am. 250. 1878).

*Echites concolor* Ham. Prodr. 31. 1825. This may refer to **Mesechites angustifolia** (Poir.) Miers, Apoc. So. Am. 230. 1878 (*Echites angustifolia* Poir. Encycl. Suppl. 2: 537. 1812).

*Echites congesta* HBK. Nov. Gen. 3: 214. 1819 = **Mandevilla congesta** (HBK.) Woodson, Ann. Mo. Bot. Gard. 20: 675. 1933.

*Echites convolvulacea* A. DC. in DC. Prodr. 8: 451. 1844 = **Mandevilla convolvulacea** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Echites cordata* A. DC. in DC. Prodr. 8: 451. 1844. This is probably referable to **Mandevilla convolvulacea** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882 (*Echites convolvulacea* A. DC. loc. cit. 1844).

*Echites coriacea* Benth. in Hook. Jour. Bot. 3: 249. 1841 = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6: 119. 1860 (*Echites geminata* R. & S. Syst. 4: 796. 1819).

*Echites corymbosa* Jacq. Enum. Pl. Carib. 13. 1760 = **Forsteronia corymbosa** (Jacq.) G. F. W. Meyer, Prim. Fl. Esseq. 134. 1818.

*Echites Coulteri* S. Wats. Proc. Am. Acad. 18: 113. 1882-83 = **Mandevilla Karwinskii** (Muell.-Arg.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882 (*Amblyanthera Karwinskii* Muell.-Arg. Linnaea 30: 426. 1860).

*Echites crassinoda* Gardn. ex Hook. Lond. Jour. Bot. 1: 544. 1842 = **Mandevilla crassinoda** (Gardn.) Woodson, Ann. Mo. Bot. Gard. 20: 703. 1933.

*Echites crassipes* A. Rich. in Sagra, Hist. Cuba 11: 91. 1850 = **Echites umbellata** Jacq. var. *crassipes* (A. Rich.) Gomez, Anal. Soc. Espan. Hist. Nat. 23: 274. 1894.

*Echites cubensis* (Muell.-Arg.) Griseb. Cat. Pl. Cub. 172. 1866 (*Rhabdadenia cubensis* Muell.-Arg. Linnaea 30: 435. 1860) = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

*Echites Cururu* Mart. in Buchn. Rep. Pharm. 101. 1830 = **Odontadenia puncticulosa** (A. Rich.) Pulle, Enum. Pl. Surinam 383. 1906 (*Echites puncticulosa* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites cuspidifera* Blake, Contr. Gray Herb. 52: 79. 1917 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites Cuyabensis* A. DC. in DC. Prodr. 8: 462. 1844 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat.

Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites cyaniphylla* Rusby, Bull. N. Y. Bot. Gard. 4: 409. 1907 = **Prestonia cyaniphylla** (Rusby) Woodson, Ann. Mo. Bot. Gard. 23: 284. 1936.

*Echites densevenulosa* Stadelm. Flora 24<sup>1</sup>: Beibl. 47. 1841 = **Odontadenia lutea** (Vell.) Mgf. in Fedde, Rep. Sp. Nov. 20: 24. 1924 (*Echites lutea* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 25. 1827).

*Echites densiflora* Pohl, ex Stadelm. Flora 24<sup>1</sup>: Beibl. 56. 1841 = **Mandevilla pycnantha** (Steud.) Woodson, Ann. Mo. Bot. Gard. 19: 60. 1932 (*Echites pycnantha* Steud. Nomencl. ed. 2. 1: 540. 1840).

*Echites denticulata* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 30. 1827 = **Prestonia denticulata** (Vell.) Woodson, Ann. Mo. Bot. Gard. 23: 328. 1936.

*Echites dichotoma* HBK. Nov. Gen. 3: 217. 1819. This apparently refers to **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites didyma* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 27. 1827 = **Prestonia didyma** (Vell.) Woodson, Ann. Mo. Bot. Gard. 23: 308. 1936.

*Echites difformis* Walt. Fl. Carol. 98. 1788 = **Trachelospermum difforme** (Walt.) A. Gray, Syn. Fl. N. Am. 2<sup>1</sup>: 85. 1878.

*Echites disadena* Miq. Stirp. Surinam. Select. 156. 1851 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites dolichopetala* Urb. Symb. Ant. 7: 335. 1912 = **Asketanthera dolichopetala** (Urb.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Echites domingensis* Jacq. Icon. Pl. Rar. 1: 6. pl. 53. 1782 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites dubia* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 50. 1827 = **Cissampelos ovalifolia** DC. Syst. 1: 537. 1818.

*Echites Dusenii* Malme, Arkiv f. Bot. 22A<sup>2</sup>: 9. 1928 = **Prestonia Dusenii** (Malme) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites Eggersii* Mgf. Notizblatt 9: 78. 1924 = **Laubertia Boissierii** A. DC. in DC. Prodr. 8: 487. 1844.

*Echites Ehrenbergii* Schlecht. Linnaea 26: 666. 1853 = **Rhabdadenia biflora** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860 (*Echites biflora* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites elegans* Benth. in Hook. Jour. Bot. 3: 249. 1841 = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860 (*Echites geminata* R. & S. Syst. 4: 795. 1819).

*Echites emarginata* Vell. Fl. Flum. 113. 1830; Icon. 3: pl. 46. 1827 = **Mandevilla erecta** (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 62. 1932 (*Echites erecta* Vell. loc. cit. 1830; loc. cit. pl. 45. 1827).

*Echites erecta* Vell. Fl. Flum. 113. 1830; Icon. 3: pl. 45. 1827 = **Mandevilla erecta** (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 62. 1932.

*Echites erecta* A. DC. in DC. Prodr. 8: 469. 1844, non Vell. = **Rhodocalyx rotundifolius** Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 173. pl. 51. 1860.

*Echites exilicaulis* Sesse & Moc. Fl. Mex. 45. 1887. Description impossible to interpret.

*Echites ferruginea* A. Rich. in Sagra, Hist. Cuba 11: 92. 1850 = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

*Echites floribunda* Sw. Prodr. 52. 1788 = **Forsteronia floribunda** (Sw.) G. F. W. Meyer, Prim. Fl. Esseq. 135. 1818.

*Echites fluminensis* A. DC. in DC. Prodr. 8: 452. 1844 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792, non R. & P).

*Echites fragrans* Stadelm. Flora 24<sup>1</sup>: Beibl. 71. 1841 = **Mandevilla fragrans** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 713. 1933.

*Echites Franciscea* A. DC. in DC. Prodr. 8: 452. 1844 = **Temnadenia violacea** (Vell.) Miers, Apoc. So. Am. 208. 1878

(*Echites violacea* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 31. 1827).

*Echites Fraseri* Willd. ex R. & S. Syst. 4: 796. 1819. The identity of this species cannot be ascertained from the ambiguous reference.

*Echites funiformis* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 29. 1827 = **Mandevilla funiformis** (Vell.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites galegiformis* Rudolph, ex Ledeb. Pl. S. Dom. 6. 1805. Reference too vague for identification.

*Echites geminata* R. & S. Syst. 4: 795. 1819 = **Odontadenia geminata** (R. & S.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 119. 1860.

*Echites glandulosa* Poir. Encycl. Suppl. 2: 537. 1812. Reference too vague for identification.

*Echites glandulosa* R. & P. Fl. Peruv. 2: 19. pl. 135. 1799 = **Mandevilla glandulosa** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 66. 1932.

*Echites glaucescens* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 358. 1844 = **Mandevilla oaxacana** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882 (*Echites Oaxacana* A. DC. in DC. Prodr. 8: 451. 1844).

*Echites glomerata* Poir. Encycl. Suppl. 2: 536. 1812. Possibly asclepiadaceous.

*Echites gracilipes* Stadelm. Flora 24<sup>1</sup>: Beibl. 22. 1841 = **Odontadenia gracilipes** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 22: 294. 1935.

*Echites gracilis* HBK. Nov. Gen. 3: 219. 1819 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites grandiflora* Desf. ex Hook. Jour. Bot. 1: 286. 1834 = **Macrosiphonia longiflora** (Desf.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 140. 1860 (*Echites longiflora* Desf. Mem. Mus. Paris 5: 275. pl. 20. 1819).

*Echites grandiflora* G. F. W. Meyer, Prim. Fl. Esseq. 131. 1818 = **Odontadenia Hoffmannseggiana** (Stend.) Woodson, in Gleason & A. C. Smith, Bull. Torrey Bot. Club 60: 392. 1933 (*Echites Hoffmannseggiana* Stend. Nomencl. ed. 2. 1: 539. 1840).

*Echites Guarantica* St. Hil. Mem. Mus. Paris 12: 324. 1825 = **Macrosiphonia longiflora** (Desf.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 140. 1860 (*Echites longiflora* Desf. Mem. Mus. Paris 5: 275. 1819).

*Echites Guianensis* A. DC. in DC. Prodr. 8: 458. 1844 = **Mandevilla subspicata** (Vahl) Mgf. Rec. Trav. Bot. Néerl. 22: 380. 1926 (*Echites subspicata* Vahl, Eclog. Am. 2: 18. 1798).

*Echites heterophylla* J. F. Gmel. Syst. 2: 437. 1791 = **Urrechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites heterophylla* Miq. Linnaea 25: 653. 1852, non Gmel. = **Elytropus chilensis** (A. DC.) Muell.-Arg. Linnaea 30: 440. 1860 (*Echites Chilensis* A. DC. in DC. Prodr. 8: 468. 1844).

*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites hirsuta* R. & P. Fl. Peruv. 2: 19. pl. 136. 1799, non A. Rich. = **Mandevilla Pavonii** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 73. 1932 (*Echites Pavonii* A. DC. in DC. Prodr. 8: 463. 1844).

*Echites hirtella* HBK. Nov. Gen. 3: 213. 1819 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites hirtiflora* A. DC. in DC. Prodr. 8: 456. 1844 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites hispida* Willd. ex R. & S. Syst. 4: 795. 1819 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites Hoffmannseggiana* Steud. Nomencl. ed. 2. 1: 539. 1840 = **Odontadenia Hoffmannseggiana** (Steud.) Woodson, in Gleason & A. C. Smith, Bull. Torrey Bot. Club 60: 392. 1933.

*Echites holosericea* Sesse & Moc. Fl. Mex. 45. 1887. Description impossible to interpret.

*Echites Hookeri* A. DC. in DC. Prodr. 8: 476. 1844. Possibly a species of *Mandevilla*. Type specimen (*Tweedie s.n.* in hb. Kew.) fragmentary.

*Echites Hulkiana* Pulle, Rec. Trav. Bot. Néerl. 9: 160. 1912 = **Prestonia acutifolia** (Benth.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895 (*Haemadictyon acutifolium* Benth. ex Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 167. 1860).

*Echites hypoglauc*a Stadelm. Flora 24<sup>1</sup>: Beibl. 23. 1841 = **Odontadenia hypoglauca (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860.**

*Echites hypoleuca* Benth. Pl. Hartw. 23. 1839 = **Macrosiphonia hypoleuca** (Benth.) Muell.-Arg. Linnaea 30: 452. 1860.

*Echites illustris* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 49. 1827 = **Mandevilla illustris** (Vell.) Woodson, Ann. Mo. Bot. Gard. 20: 727. 1933.

*Echites insignis* Spreng. Syst. 1: 632. 1825. Possibly refers to *Odontadenia Hoffmannseggiana* (Steud.) Woodson.

*Echites istmica* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 39. 1827 = *Condyllocarpon* sp.

*Echites jamaicensis* Griseb. Fl. Brit. W. I. 416. 1861 = **Urechites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites japurensis* Stadelm. Flora 24<sup>1</sup>: Beibl. 19. 1841. = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites jasminiflora* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 357. 1844 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites javitensis* HBK. Nov. Gen. 3: 220. 1819 = **Mandevilla javitensis** (HBK.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites Karwinskii* (Muell.-Arg.) Miers, Apoc. So. Am. 206. 1878 (*Amblyanthera Karwinskii* Muell.-Arg. Linnaea 30: 426. 1860) = **Mandevilla Karwinskii** (Muell.-Arg.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Echites lanata* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 359. 1844. Possibly refers to *Mandevilla subsagittata* (R. & P.) Woodson. The type specimen evidently has been lost.

*Echites lanuginosa* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 357. 1844 = **Macrosiphonia lanuginosa** (Mart. & Gal.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Echites lanuginosa* Sesse & Moc. Fl. Mex. 44. 1887, non Mart. & Gal. Impossible to interpret.

*Echites lappulacea* Lam. Encycl. 2: 341. 1786 = **Anechites lappulacea** (Lam.) Miers, Apoc. So. Am. 237. 1878.

*Echites lasiocarpa* A. DC. in DC. Prodr. 8: 463. 1844 = **Mandevilla lasiocarpa** (A. DC.) Malme, Bihang till K. Sv. Vet. Akad. Handl. Afd. III. 24<sup>10</sup>: 25. 1899.

*Echites lateriflora* Sesse & Moc. La Naturaleza II. 1: Suppl. 28. 1888. Impossible to interpret.

*Echites Laurentiae-disca* Rusby, Descr. So. Am. Pl. 85. 1920 = **Prestonia acutifolia** (Benth.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895 (*Haemadictyon acutifolium* Benth. ex Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 167. 1860).

*Echites laxa* R. & P. Fl. Peruv. 2: 19. pl. 134b. 1799 = **Mandevilla laxa** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 68. 1932.

*Echites leptoloba* Stadelm. Flora 24<sup>1</sup>: Beibl. 15. 1841 = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites leptophylla* A. DC. in DC. Prodr. 8: 455. 1844 = **Mandevilla leptophylla** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites Lindeniana* (Muell.-Arg.) Griseb. Cat. Pl. Cub. 173. 1866 (*Rhabdadenia Lindeniana* Muell.-Arg. Linnaea 30: 437. 1860) = **Angadenia Lindeniana** (Muell.-Arg.) Miers, Apoc. So. Am. 180. 1878.

*Echites linearifolia* Ham. Prodr. 31. 1825 = **Mesechites angustifolia** (Poir.) Miers, Apoc. So. Am. 230. 1878 (*Echites angustifolia* Poir. Encycl. Suppl. 2: 537. 1812).

*Echites linearifolia* Stadelm. Flora 24<sup>1</sup>: Beibl. 18. 1841, non Ham. = **Mandevilla leptophylla** (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites leptophylla* A. DC. in DC. Prodr. 8: 455. 1844).



*Echites linearis* Vell. Fl. Flum. 111. 1830; Icon. 3: pl. 36. 1827. Possibly referable to *Forsteronia*.

*Echites longiflora* Desf. Mem. Mus. Paris 5: 275. 1819 = **Macrosiphonia longiflora** (Desf.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 140. 1860.

*Echites longiflora* Ekm. & Helwig, Arkiv f. Bot. 22A<sup>10</sup>: 45. 1929, non Desf. = **Asketanthera Ekmaniana** Woodson, Ann. Mo. Bot. Gard. 23: 267. 1936.

*Echites longifolia* Sesse & Moc. Fl. Mex. 45. 1887. May possibly refer to *E. tuxtlensis* Standl.

*Echites lucida* R. & S. Syst. 4: 795. 1819 = **Odontadenia nitida** (Vahl) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860 (*Echites nitida* Vahl, Eclog. 2: 19. pl. 13. 1798).

*Echites lutea* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 25. 1827 = **Odontadenia lutea** (Vell.) Mgf. in Fedde, Rep. Sp. Nov. 20: 24. 1924.

*Echites macrantha* R. & S. Syst. 4: 795. 1819, non Spreng. = **Odontadenia Hoffmannseggiana** (Steud.) Woodson, in Gleason & A. C. Smith, Bull. Torrey Bot. Club 60: 392. 1933 (*Echites Hoffmannseggiana* Steud. Nomencl. ed. 2. 1: 539. 1840).

*Echites macrocalyx* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 160. 1860 = **Peltastes peltatus** (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932 (*Echites peltata* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 32. 1827).

*Echites* ? *macrocarpa* A. Rich. in Sagra, Hist. Cuba 11: 94. 1850, non Wall. = **Catalpa macrocarpa** (A. Rich.) Ekman, in Urb. Symb. Ant. 9: 254. 1924.

*Echites macrophylla* HBK. Nov. Gen. 3: 218. 1819, non Roxb. = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites macrophylla* A. Zahlbr. Ann. K. K. Naturh. Hofmus. Wien 7: 5. 1892, nec HBK., nec Roxb. = **Mandevilla subpaniculata** Woodson, Ann. Mo. Bot. Gard. 19: 71. 1932.

*Echites Macrosiphon* Torr. Bot. Mex. Bound. Surv. 158. pl. 43. 1859 = **Macrosiphonia Macrosiphon** (Torr.) A. A. Heller, Muhlenbergia 1: 2. 1900.

*Echites macrostoma* Benth. in Hook. Jour. Bot. 3: 248. 1841 = **Rhabdadenia macrostoma** (Benth.) Muell.-Arg. Linnaea 30: 435. 1860.

*Echites maculata* (Descourt.) A. DC. in DC. Prodr. 8: 474. 1844 (*Apocynum maculatum* Descourt. Fl. Med. Antill. 3: 176. pl. 190. 1827). Probably referable to the asclepiadaceous genus *Marsdenia*.

*Echites madida* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 42. 1827. Possibly referable to *Mandevilla*.

*Echites Mansoana* A. DC. in DC. Prodr. 8: 448. 1844 = **Mesechites Mansoana** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 20: 636. 1933.

*Echites mapirensis* H. Winkl. in Fedde, Rep. Sp. Nov. 7: 113. 1909. Possibly referable to *Mesechites acuminata* (R. & P.) Muell.-Arg. Linnaea 30: 446. 1860. The type specimen (*Buch-tien* 1954) has not been available for study.

*Echites Maranhensis* G. Don, Gen. Hist. 4: 74. 1838 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites Martiana* Stadelm. Flora 24<sup>1</sup>: Beibl. 31. 1841 = **Mandevilla Martiana** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 702. 1933.

*Echites Martii* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 155. 1860 = **Prestonia coalita** (Vell.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites coalita* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 40. 1827).

*Echites Maximiliana* Stadelm. Flora 24<sup>1</sup>: Beibl. 43. 1841 = **Temnadenia violacea** (Vell.) Miers, Apoc. So. Am. 208. 1878 (*Echites violacea* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 31. 1827).

*Echites Meg'agros* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 33. 1827 = **Prestonia Meg'agros** (Vell.) Woodson, Ann. Mo. Bot. Gard. 23: 329. 1936.

*Echites membranacea* A. DC. in DC. Prodr. 8: 457. 1844 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites mexicana* (Muell.-Arg.) Miers, Apoc. So. Am. 205. 1878 (*Amblyanthera mexicana* Muell.-Arg. Linnaea 30: 424. 1860) = **Mandevilla mexicana** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 65. 1932.

*Echites microcalyx* A. DC. in DC. Prodr. 8: 456. 1844 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites microphylla* Stadelm. Flora 24<sup>1</sup>: Beibl. 35. 1841 = **Mandevilla funiformis** (Vell.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites funiformis* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 29. 1827).

*Echites minima* Britton & Wilson, Mem. Torrey Bot. Club 16: 94. 1920 = **Mesechites minima** (Britton & Wilson) Woodson, Ann. Mo. Bot. Gard. 19: 386. 1932.

*Echites mollissima* HBK. Nov. Gen. 3: 218. 1819 = **Mandevilla mollissima** (HBK.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites montana* HBK. Nov. Gen. 3: 213. 1819 = **Mandevilla montana** (HBK.) Mgf. Notizblatt 9: 82. 1924.

*Echites mucronata* R. & S. Syst. 4: 796. 1819 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites ? muricata* A. DC. in DC. Prodr. 8: 474. 1844. Based upon Descourt. Fl. Med. Antill. 3: 171. pl. 189. 1827. Evidently asclepiadaceous.

*Echites myrtifolia* R. & S. Syst. 4: 795. 1819, non Poir. = **Mesechites rosea** (A. DC.) Miers, Apoc. So. Am. 232. 1878 (*Echites rosea* A. DC. in DC. Prodr. 8: 450. 1844).

*Echites neriantha* Griseb. Fl. Brit. W. I. 415. 1861 = **Ur-echites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites nitida* Vahl, Eclog. 2: 19. pl. 13. 1798 = **Odontadenia nitida** (Vahl) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 118. 1860.

*Echites nodosa* R. & S. Syst. 4: 796. 1819. Based upon a sterile specimen which is impossible to determine accurately.

*Echites nutans* Anders. Trans. Soc. Arts London 25: 203. 1807 = **Prestonia quinquangularis** (Jacq.) Spreng. Syst. 1: 637. 1825 (*Echites quinquangularis* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites Oaxacana* A. DC. in DC. Prodr. 8: 451. 1844 = **Mandevilla oaxacana** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Echites oblongifolia* Ham. Prodr. 30. 1825. Perhaps referable to *Mesechites*.

*Echites obovata* Nees, ex Steud. Nomencl. ed. 2. 1: 540. 1840. Based upon *E. variegata* Schrad. Goett. Gel. Anz. 1: 707. 1821, a *nomen subnudum* incapable of interpretation.

*Echites obovata* Sesse & Moc. Fl. Mex. 43. 1887. May refer to *Urechites lutea* (L.) Britton.

*Echites obtusifolia* Sesse & Moc. Fl. Mex. 45. 1887. Impossible to interpret.

*Echites odorifera* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 28. 1827. The plate cited has somewhat the aspect of a *Temnadenia*, but is not capable of identification.

*Echites ornata* Hoehne, Comm. Linh. Electr. Estrat. Matto Grosso, Anexo 5, Bot. 6: 82. pls. 120; 131, fig. 1. 1915 = **Temnadenia ornata** (Hoehne) Woodson, Ann. Mo. Bot. Gard. 19: 383. 1932.

*Echites* ? *ovalifolia* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834. Type specimen (*Tweedie s.n.* in Hb. Kew.) fragmentary, possibly asclepiadaceous.

*Echites ovalifolia* Poir. Encycl. Suppl. 2: 535. 1812. Considered by Miers (Apoc. So. Am. 248. 1878) to be a *Forsteronia*. If so, it possibly represents *F. spicata* (Jacq.) G. F. W. Meyer, of which, however, we have no authenticated specimens from Hispaniola.

*Echites ovalis* Mgf. Notizblatt 9: 79. 1924 = **Allomarkgrafia ovalis** (Mgf.) Woodson, Ann. Mo. Bot. Gard. 19: 45. 1932.

*Echites pallida* Miers, Apoc. So. Am. 195. 1878 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites paludosa* Vahl, *Eclog.* 2: 19. 1798 = **Rhabdadenia biflora** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 175. 1860 (*Echites biflora* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites pandurata* A. DC. in DC. Prodr. 8: 458. 1844 = **Fernaldia pandurata** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

*Echites paniculata* Poir. Encycl. Suppl. 2: 536. 1811. Diagnosis impossible to interpret.

*Echites parviflora* Sesse & Moc. Fl. Mex. 44. 1887. Impossible to interpret.

*Echites pastorum* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 52. 1841 = **Mandevilla tenuifolia** (Mikan) Woodson, Ann. Mo. Bot. Gard. 20: 679. 1933 (*Echites tenuifolia* Mikan, Fl. & Faun. Bras. fasc. 3. 1820).

*Echites Pavonii* A. DC. in DC. Prodr. 8: 463. 1844 = **Mandevilla Pavonii** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 73. 1932.

*Echites peduncularis* Stadelm. Flora 24<sup>1</sup>: Beibl. 54. 1841 = **Mandevilla tenuifolia** (Mikan) Woodson, Ann. Mo. Bot. Gard. 20: 679. 1933 (*Echites tenuifolia* Mikan, Fl. & Faun. Bras. fasc. 3. 1820).

*Echites peltata* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 32. 1827 = **Peltastes peltatus** (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932.

*Echites peltigera* Stadelm. Flora 24<sup>1</sup>: Beibl. 21. 1841 = **Stipecoma peltigera** (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 176. 1860.

*Echites petraea* St. Hil. Mem. Mus. Paris 12: 322. 1825 = **Macrosiphonia petraea** (St. Hil.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 168. 1895.

*Echites Picardae* Urb. Symb. Ant. 5: 466. 1908 = **Asketanthera Picardae** (Urb.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Echites pilosa* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 38. 1827 = **Forsteronia pilosa** (Vell.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 99. 1860.

*Echites pinguifolia* Standl. Field Mus. Publ. Bot. 8: 35. 1930

= **Fernaldia pandurata** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

*Echites pinifolia* St. Hil. Mem. Mus. Paris 12: 325. 1825 = **Macrosiphonia petraea** (St. Hil.) K. Sch. var. **minor** (Hook.) Woodson, Ann. Mo. Bot. Gard. 23: 376. 1936 (*Echites grandiflora* Desf. var. **minor** Hook. Jour. Bot. 1: 286. 1834).

*Echites plicata* A. DC. in DC. Prodr. 8: 454. 1844 = **Peltastes peltatus** (Vell.) Woodson, Ann. Mo. Bot. Gard. 19: 376. 1932 (*Echites peltata* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 32. 1827).

*Echites Pohliana* Stadelm. Flora 24<sup>1</sup>: Beibl. 73. 1841 = **Mandevilla velutina** (Mart.) Woodson var. **angustifolia** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 23: 376. 1936 (*Echites Pohliana* Stadelm. var.  $\alpha$  **angustifolia** Stadelm. loc. cit. 1841).

*Echites portobellensis* Beurl. Vet. Akad. Handl. Stockh. 137. 1854 (1856) = **Prestonia portobellensis** (Beurl.) Woodson, Ann. Mo. Bot. Gard. 18: 553. 1931.

*Echites Prieurei* A. DC. in DC. Prodr. 8: 458. 1844 = **Mandevilla subspicata** (Vahl) Mgf. Rec. Trav. Bot. Néerl. 22: 380. 1926 (*Echites subspicata* Vahl, Eclog. 2: 18. 1798).

*Echites psidiifolia* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 46. 1841. Possibly refers to *Odontadenia*. The type specimen has apparently been lost.

*Echites ptarmica* Poepp. Gen. 3: 69. pl. 278. 1845 = **Elytropus chilensis** (A. DC.) Muell.-Arg. Linnaea 30: 440. 1860 (*Echites Chilensis* A. DC. in DC. Prodr. 8: 468. 1844).

*Echites puberula* Michx. Fl. Bor. Am. 1: 120. 1803 = **Trachelospermum difforme** (Walt.) A. Gray, Syn. Fl. N. Am. 2: 85. 1878 (*Echites difformis* Walt. Fl. Carol. 98. 1788).

*Echites pubescens* Hook. & Arn. Bot. Beechey Voy. 34. 1830, non R. & S. = **Elytropus chilensis** (A. DC.) Muell.-Arg. Linnaea 30: 440. 1860 (*Echites Chilensis* A. DC. in DC. Prodr. 8: 468. 1844).

*Echites pubescens* R. & S. Syst. 4: 796. 1819 = **Mandevilla congesta** (HBK.) Woodson, Ann. Mo. Bot. Gard. 20: 675. 1933 (*Echites congesta* HBK. Nov. Gen. 3: 214. 1819).

*Echites pubiflora* G. Don, Gen. Hist. 4: 73. 1838 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites pulchella* Gardn. ex Hook. Icon. Pl. 5: pl. 470. 1842 = **Mandevilla spigeliaeflora** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 736. 1933 (*Echites* (?) *spigeliaeflora* Stadelm. Flora 24<sup>1</sup>: Beibl. 58. 1841).

*Echites puncticulosa* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792 = **Odontadenia puncticulosa** (A. Rich.) Pulle, Enum. Pl. Surinam, 383. 1906.

*Echites pycnantha* Steud. ex A. DC. in DC. Prodr. 8: 469. 1844 = **Mandevilla pycnantha** (Steud.) Woodson, Ann. Mo. Bot. Gard. 19: 60. 1932.

*Echites quinquangularis* Jacq. Enum. Pl. Carib. 13. 1760 = **Prestonia quinquangularis** (Jacq.) Spreng. Syst. 1: 637. 1825.

*Echites repens* Jacq. Enum. Pl. Carib. 13. 1760 = **Mesechites repens** (Jacq.) Miers, Apoc. So. Am. 229. 1878.

*Echites revoluta* A. DC. in DC. Prodr. 8: 457. 1844 = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites revoluta* Sesse & Moc. Fl. Mex. 44. 1887. Impossible to interpret.

*Echites Richardi* R. & S. Syst. 4: 391. 1819 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792).

*Echites* (?) *Riedelii* (Muell.-Arg.) Malme, Bull. Herb. Boiss. II. 4: 196. 1904 (*Haemadictyon Riedelii* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 170. 1860) = **Prestonia Riedelii** (Muell.-Arg.) Mgf. in Fedde, Rep. Spec. Nov. 20: 26. 1924.

*Echites rigida* Rusby, Mem. N. Y. Bot. Gard. 7: 325. 1927 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites riparia* HBK. Nov. Gen. 3: 214. 1819 = **Mandevilla riparia** (HBK.) Woodson, Ann. Mo. Bot. Gard. 19: 58. 1932.

*Echites Rosa-campestris* Endl. in Harting, Parad. Vindob. 1: pl. 51. 1844-47 = **Mandevilla illustris** (Vell.) Woodson, Ann. Mo. Bot. Gard. 20: 727. 1933 (*Echites illustris* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 49. 1827).

*Echites Rosana* Donn. Sm. Bot. Gaz. 40: 6. 1905 = **Mandevilla Rosana** (Donn. Sm.) Woodson, Ann. Mo. Bot. Gard. 20: 652. 1932.

*Echites rosea* A. DC. in DC. Prodr. 8: 450. 1844 = **Mesechites rosea** (A. DC.) Miers, Apoc. So. Am. 232. 1878.

*Echites rubricaulis* Poir. Encycl. Suppl. 2: 535. 1812. Apparently refers to *Mesechites trifida* (Jacq.) Muell.-Arg. or a related species.

*Echites Rugeliana* Urb. Symb. Ant. 5: 465. 1908 = **Asketanthera calycosa** (A. Rich.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932 (*Echites calycosa* A. Rich. in Sagra, Hist. Cuba 11: 94. 1850).

*Echites rugellosa* A. Rich. Actes Soc. Nat. Hist. Paris 1: 107. 1792. Incapable of identification.

*Echites rugosa* Benth. in Hook. Jour. Bot. 3: 248. 1841 = **Mandevilla rugosa** (Benth.) Woodson, Ann. Mo. Bot. Gard. 19: 384. 1932.

*Echites sagittata* Poir. Encycl. Suppl. 2: 537. 1812. Incapable of identification. Perhaps referable to *Mandevilla subsagittata* (R. & P.) Woodson.

*Echites Sagraei* A. DC. in DC. Prodr. 8: 450. 1844 = **Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. loc. cit. 447. 1844).

*Echites salicifolia* Raf. New Fl. N. Am. 4: 59. 1836, non Willd. = **Trachelospermum difforme** (Walt.) A. Gray, Syn. Fl. N. Am. 2: 85. 1878 (*Echites difformis* Walt. Fl. Carol. 98. 1788).

*Echites salicifolia* Willd. ex R. & S. Syst. 4: 796. 1819 = **Allemanda cathartica** L. Mant. 214. 1771.

*Echites sancta* Stadelm. Flora 24<sup>1</sup>: Beibl. 59. 1841 = **Mandevilla sancta** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 726. 1933.

*Echites Sanctae-Crucis* S. Moore, Trans. Linn. Soc. Bot. II.



4: 396. 1895 = **Mesechites Sanctae-Crucis** (S. Moore) Woodson, Ann. Mo. Bot. Gard. 19: 387. 1932.

*Echites Sanctae-Martae* Rusby, Descr. So. Am. Pl. 85. 1920 = **Laubertia Sanctae-Martae** (Rusby) Woodson, Ann. Mo. Bot. Gard. 18: 555. 1931.

*Echites sanguinolenta* Tussac, Fl. Ant. 95. pl. 11. 1808 = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites scabra* R. & S. Syst. 4: 795. 1819 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites secunda* Sesse & Moc. Fl. Mex. 44. 1887. May refer to *Mandevilla subsagittata* (R. & P.) Woodson.

*Echites secundiflora* A. DC. in DC. Prodr. 8: 457. 1844 = **Mandevilla subsagittata** (R. & P.) Woodson (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites semidigyna* Berg. Verh. Zeeusch. Gen. Wetens. 3: 583. 1773. Probably a species of *Tabernaemontana*.

*Echites sessilis* Vell. Fl. Flum. 111. 1830; Icon. 3: pl. 35. 1827. Incapable of identification. Supposed by Mueller to be a *Malouetia*; a *Thyrsanthus* (*Forsteronia*) according to Miers.

*Echites Smithii* Greenm. Proc. Am. Acad. 40: 29. 1904 = **Mandevilla mexicana** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 65. 1932 (*Amblyanthera mexicana* Muell.-Arg. Linnaea 30: 424. 1860).

*Echites speciosa* HBK. Nov. Gen. 3: 219. 1819 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Echites spectabilis* Stadelm. Flora 24<sup>1</sup>: Beibl. 44. 1841 = **Macropharynx spectabilis** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites spicata* Jacq. Enum. Pl. Carib. 13. 1760 = **Forsteronia spicata** (Jacq.) G. F. W. Meyer, Prim. Fl. Esseq. 135. 1818.

*Echites* (?) *spigeliaeflora* Stadelm. Flora 24<sup>1</sup>: Beibl. 58. 1841 = **Mandevilla spigeliaeflora** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 20: 736. 1933.

*Echites splendens* Hook. f. Bot. Mag. n.s. 16: pl. 3976. 1842 = **Mandevilla splendens** (Hook. f.) Woodson, Ann. Mo. Bot. Gard. 20: 707. 1933.

*Echites Stadelmeyeri* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 29. 1841 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895.

*Echites stellaris* Lindl. Bot. Reg. 20: pl. 1664. 1834 = **Temnadenia stellaris** (Lindl.) Miers, Apoc. So. Am. 210. 1878.

*Echites stellulifera* Lem. Jard. Fleur. 1: pl. 67. 1851. Apparently referable to *Temnadenia stellaris* (Lindl.) Miers.

*Echites suaveolens* (Lindl.) A. DC. in DC. Prodr. 8: 452. 1844 (*Mandevilla suaveolens* Lindl. Bot. Reg. n.s. 3: pl. 7. 1840 = **Mandevilla laxa** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 68. 1932 (*Echites laxa* R. & P. Fl. Peruv. 2: 19. pl. 134b. 1799).

*Echites suaveolens* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 356. 1844, non A. DC. = **Macrosiphonia hypoleuca** (Benth.) Muell.-Arg. Linnæa 30: 452. 1860 (*Echites hypoleuca* Benth. Pl. Hartw. 23. 1839).

*Echites subcarnosa* Benth. in Hook. Jour. Bot. 3: 247. 1841 = **Mandevilla subcarnosa** (Benth.) Woodson, in Gleason, Bull. Torrey Bot. Club 58: 453. 1931.

*Echites subcordata* Sesse & Moc. Fl. Mex. 44. 1887. Impossible to interpret.

*Echites suberecta* Jacq. Enum. Pl. Carib. 13. 1760 = **Ur-echites lutea** (L.) Britton, Bull. N. Y. Bot. Gard. 5: 316. 1907 (*Vinca lutea* L. Cent. II. Pl. 12. 1756).

*Echites suberosa* Vell. Fl. Flum. 111. 1830; Icon. 3: pl. 34. 1827 = **Prestonia denticulata** (Vell.) Woodson, Ann. Mo. Bot. Gard. 23: 328. 1936 (*Echites denticulata* Vell. loc. cit. 110. 1830; Icon. 3: pl. 30. 1827).

*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799 = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932.

*Echites subsessilis* A. DC. in DC. Prodr. 8: 451. 1844 = **Mandevilla subsessilis** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 59. 1932.

*Echites subspicata* Vahl, *Eclog.* 2: 18. 1798 = **Mandevilla subspicata** (Vahl) Mgf. *Rec. Trav. Bot. Néerl.* 22: 380. 1926.

*Echites sulphurea* Vell. *Fl. Flum.* 109. 1830; *Icon.* 3: *pl.* 26. 1827. Possibly referable to *Prestonia coalita* (Vell.) Woodson.

*Echites surinamensis* Miq. *Stirp. Surinam. Select.* 155. 1850 = **Mesechites trifida** (Jacq.) Muell.-Arg. in *Mart. Fl. Bras.* 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. *Enum. Pl. Carib.* 13. 1760).

*Echites sylvestris* A. DC. in DC. *Prodr.* 8: 464. 1844 = **Odontadenia Hoffmannseggiana** (Steud.) Woodson, in Gleason & A. C. Smith, *Bull. Torrey Bot. Club* 60: 392. 1933 (*Echites Hoffmannseggiana* Steud. *Nomencl. ed.* 2. 1: 539. 1840).

*Echites symphitocarpa* G. F. W. Meyer, *Prim. Fl. Esseq.* 132. 1818 = **Mandevilla symphitocarpa** (G. F. W. Meyer) Woodson, *Ann. Mo. Bot. Gard.* 19: 70. 1932.

*Echites syphilitica* L.f. *Suppl.* 167. 1781. Incapable of identification.

*Echites tenuicaulis* Stadelm. *Flora* 24<sup>1</sup>: Beibl. 40. 1841 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, *Nat. Pflanzenfam.* 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. *Syst.* 4: 795. 1819).

*Echites tenuifolia* Mikan, *Fl. & Faun. Bras. fasc.* 3. 1820 = **Mandevilla tenuifolia** (Mikan) Woodson, *Ann. Mo. Bot. Gard.* 20: 679. 1933.

*Echites thyrsoides* Vell. *Fl. Flum.* 111. 1830; *Icon.* 3: *pl.* 37. 1827 = **Forsteronia thyrsoides** (Vell.) Muell.-Arg. in *Mart. Fl. Bras.* 6<sup>1</sup>: 105. 1860.

*Echites tomentosa* Raf. *Fl. Ludovic.* 46. 1819, non Vahl. Perhaps referable to *Trachelospermum difforme* (Walt.) A. Gray.

*Echites tomentosa* Vahl, *Symb. Bot.* 3: 44. 1794 = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, *Nat. Pflanzenfam.* 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. *Actes Soc. Hist. Nat. Paris* 1: 107. 1792).

*Echites torosa* Jacq. *Enum. Pl. Carib.* 13. 1760 = **Mandevilla torosa** (Jacq.) Woodson, *Ann. Mo. Bot. Gard.* 19: 64. 1932.

*Echites torulosa* L. *Sp. Pl. ed.* 2. 307. 1762 = **Mandevilla torosa** (Jacq.) Woodson, *Ann. Mo. Bot. Gard.* 19: 64. 1932 (*Echites torosa* Jacq. *Enum. Pl. Carib.* 13. 1760).

*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860.

*Echites tropaeolifolia* A. DC. in DC. Prodr. 8: 447. 1844 = **Stipecoma peltigera** (Stadelm.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 176. 1860 (*Echites peltigera* Stadelm. Flora 24<sup>1</sup>: Beibl. 21. 1841).

*Echites tubiflora* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 358. 1844 = **Mandevilla tubiflora** (Mart. & Gal.) Woodson, Ann. Mo. Bot. Gard. 19: 52. 1932.

*Echites tubulosa* Benth. in Hook. Jour. Bot. 3: 249. 1841 = **Mesechites trifida** (Jacq.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 151. 1860 (*Echites trifida* Jacq. Enum. Pl. Carib. 13. 1760).

*Echites Tweediana* Hieron. Bol. Acad. Nac. Cordova 4: 370. 1881. Probably referable to *Mandevilla erecta* (Vell.) Woodson.

*Echites umbellata* Sesse & Moc. Fl. Mex. 43. 1887, non Jacq. Apparently refers to a species of *Thenardia*.

*Echites undulata* Sesse & Moc. Fl. Mex. 44. 1887. Impossible to interpret.

*Echites uniflora* Sesse & Moc. La Naturaleza II. 1: Suppl. 28. 1888. Impossible to interpret.

*Echites Valenzuelana* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850 = **Neobrcea Valenzuelana** (A. Rich.) Urb. Symb. Ant. 9: 241. 1924.

*Echites varia* Stadelm. Flora 24<sup>1</sup>: Beibl. 17. 1841 = **Temnadenia stellaris** (Lindl.) Miers, Apoc. So. Am. 210. 1878 (*Echites stellaris* Lindl. Bot. Reg. 20: pl. 1664. 1835).

*Echites variegata* Schrad. Goett. Gel. Anz. 1: 707. 1821. Perhaps referable to *Prestonia agglutinata* (Jacq.) Woodson.

*Echites Vauthieri* A. DC. in DC. Prodr. 8: 457. 1844 = **Prestonia coalita** (Vell.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites coalita* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 40. 1827).

*Echites Velame* St. Hil. Bull. Soc. Phil. 77. 1824 = **Macrosiphonia Velame** (St. Hil.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 138. 1860.

*Echites Velloziana* A. DC. in DC. Prodr. 8: 474. 1844 =

**Forsteronia Velloziana** (A. DC.) Woodson, Ann. Mo. Bot. Gard. 21: 622. 1934.

*Echites velutina* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 72. 1841 = **Mandevilla velutina** (Mart.) Woodson, Ann. Mo. Bot. Gard. 20: 731. 1933.

*Echites venenosa* Stadelm. Flora 24<sup>1</sup>: Beibl. 66. 1841 = **Mandevilla illustris** (Vell.) Woodson, Ann. Mo. Bot. Gard. 20: 727. 1933 (*Echites illustris* Vell. Fl. Flum. 114. 1830; Icon. 3: pl. 49. 1827).

*Echites Veraguasensis* Seem. Bot. Voy. Herald, 168. 1854 = **Mandevilla veraguasensis** (Seem.) Hemsl. Biol. Centr.-Am. Bot. 2: 317. 1882 (where misspelled *veraguensis*).

*Echites verrucosa* R. & S. Syst. 4: 795. 1819 = **Odontadenia verrucosa** (R. & S.) K. Sch. ex Mgf. in Pulle, Fl. Surinam 4: 53. 1932.

*Echites versicolor* Mart. ex Stadelm. Flora 24<sup>1</sup>: Beibl. 38. 1841 = **Mandevilla scabra** (R. & S.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites scabra* R. & S. Syst. 4: 795. 1819).

*Echites verticillata* Sesse & Moc. Fl. Mex. 43. 1887. The authors propose two species under the same specific adjective: one reported from Mexico and one from Porto Rico. Both are impossible to interpret.

*Echites violacea* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 31. 1827 = **Temnadenia violacea** (Vell.) Miers, Apoc. So. Am. 208. 1878.

*Echites virescens* St. Hil. Bull. Soc. Phil. 77. 1824 = **Macrosiphonia virescens** (St. Hil.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 139. 1860.

*Echites* (?) *xanthostoma* Stadelm. Flora 24<sup>1</sup>: Beibl. 55. 1841 = **Mandevilla coccinea** (Hook. & Arn.) Woodson, Ann. Mo. Bot. Gard. 20: 734. 1933 (*Echites coccinea* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834).

*Echites Zuccariniana* Stadelm. Flora 24<sup>1</sup>: Beibl. 76. 1841 = **Odontadenia lutea** (Vell.) Mgf. in Fedde, Rep. Sp. Nov. 20: 24. 1924 (*Echites lutea* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 25. 1827).

## XXI. TEMNADENIA Miers, char. emend.

**Temnadenia** Miers, Apoc. So. Am. 207. 1878, in part.

Lactescent, fruticose lianas. Stems volubile, rarely suberect, terete; branches alternate. Leaves opposite, petiolate to sessile, entire, penninerved, eglandular, the petioles somewhat girdling at the nodes into a slightly dilated, minutely appendiculate, stipular ring. Inflorescence lateral, infrequently subterminal, alternate, scorpioid; peduncle di- or trichotomously compound, infrequently very obscurely so, bearing several to numerous relatively showy, rose or purplish, rarely greenish flowers. Calyx 5-parted, the lobes equal to subequal, imbricated, cleft nearly to the receptacle, bearing within solitary, opposite, more or less erose or lacerate squamellae. Corolla salverform to infundibuliform, the tube not appendiculate nor annulate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, included, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the fusiform-subcapitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or somewhat concrescent at the base. Follicles 2, apocarpous, terete, dehiscing along the ventral suture, containing many dry, rostrate, apically comose seeds.

Type species: *Temnadenia violacea* (Vell.) Miers, Apoc. So. Am. 208. 1878.

## KEY TO THE SPECIES

- a. Corolla salverform, 2.5–4.0 cm. long; inflorescence dichotomous, usually repeatedly so, rarely trichotomous.
- b. Corolla bright yellow, minutely and densely ferruginous-tomentulose without; plants of Colombia.....1. *T. stenantha*
- bb. Corolla cream suffused with maroon or rose in the throat, glabrous without; species of southern Brazil.
- c. Plants puberulent or hispidulous to glabrate; leaves ovate-elliptic; inflorescence relatively congested, dichotomous.....2. *T. stellaris*
- cc. Plants glabrous; leaves oblong-lanceolate; inflorescence repeatedly and irregularly di- or trichotomous, relatively lax.....3. *T. ornata*
- aa. Corolla infundibuliform, 5–6 cm. long, crimson-purple to rose; inflorescence obscurely dichotomous to essentially simple.....4. *T. violacea*

1. *Temnadenia stenantha* Woodson, Ann. Mo. Bot. Gard. 21: 613. 1934.

Stems relatively stout, minutely ferruginous-tomentulose when young, eventually becoming glabrate; leaves opposite, petiolate, oblong-elliptic, apex shortly acuminate, base broadly obtuse, 11–13 cm. long, 4.5–5.0 cm. broad, firmly membranaceous to subcoriaceous, glabrous above, beneath minutely and inconspicuously puberulent toward the base and otherwise glabrous; petioles 1.7–1.9 cm. long, minutely ferruginous-puberulent; inflorescence di- or trichotomous, bearing 20–25 rather mediocre, bright yellow flowers, minutely and irregularly ferruginous-tomentulose throughout, conspicuously surpassing the subtending leaves; pedicels 1.0–1.25 cm. long; bracts minutely lanceolate, 0.1–0.3 cm. long; calyx-lobes ovate-lanceolate, acute to acuminate, 0.35–0.53 cm. long, slightly foliaceous, minutely ferruginous-puberulent to -papillate without, the squamellae obscurely bifid; corolla salverform, minutely ferruginous-tomentulose without, the tube 2.5–2.7 cm. long, about 0.2 cm. in diameter at the base, slightly dilated toward the orifice, the lobes obliquely obovate-oblong, 1.0–1.1 cm. long, ascending or slightly spreading; stamens inserted somewhat below midway within the corolla-tube, the anthers elliptic-sagittate, 0.7–0.75 cm. long, densely villosulous-barbate dorsally; ovary ovoid-oblongoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries separate, slightly surpassing the ovary; follicles unknown.

COLOMBIA: BOYACA: on edge of high forest, region of Mt. Chapon, alt. 7000 ft., June 17, 1932, *Lawrance 341* (NY, TYPE, MBG, photograph and analytical drawings).

2. *Temnadenia stellaris* (Lindl.) Miers, Apoc. So. Am. 210. 1878.

*Echites stellaris* Lindl. Bot. Reg. 20: *pl.* 1664. 1835; A. DC. in DC. Prodr. 8: 457. 1844.

*Echites varia* Stadelm. Flora 24<sup>1</sup>: Beibl. 17. 1841; A. DC. loc. cit. 455. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 157. *pl.* 47. 1860.

*Echites Franciscea* A. DC. acc. to Lindl. Bot. Reg. n.s. 10: *pl.* 24. 1847, not A. DC. loc. cit. 452. 1844.

*Echites Franciscea* A. DC. var. *pallidiflora* Hook. f. Bot. Mag. 76: pl. 4547. 1850.

*Echites varia* Stadelm. a. *purpurea* Muell.-Arg. loc. cit. 158. 1860.

*Echites varia* Stadelm. b. *rosea* Muell.-Arg. loc. cit. 1860.

*Echites varia* Stadelm. c. *sulphurea* Muell.-Arg. loc. cit. 1860.

*Temnadenia bicrura* Miers, loc. cit. 208. 1878.

*Temnadenia pallidiflora* (Hook.) Miers, loc. cit. 211. 1878.

*Temnadenia Franciscea* (Lindl.) Miers, loc. cit. 212. 1878, not as to A. DC. loc. cit. 452. 1844.

Stems relatively slender, hispidulous to puberulent, eventually glabrate; leaves opposite, petiolate, ovate-elliptic, apex acuminate, base obtuse to rounded, 6–15 cm. long, 3–7 cm. broad, firmly membranaceous, above minutely bullate-strigillose to glabrate, beneath minutely puberulent; petioles 0.5–0.8 cm. long, puberulent; inflorescence dichotomous, usually equalling or somewhat surpassing the subtending leaves, softly puberulent throughout, bearing 10–30 congested, cream-colored flowers suffused with maroon in the tube and orifice; pedicels 0.8–1.0 cm. long, somewhat accrescent in fruit; bracts 0.2–1.0 cm. long, scarious to more or less foliaceous below; calyx-lobes ovate-lanceolate, acuminate, 0.4–0.6 cm. long, puberulent-papillate without, the squamellae deltoid, truncate, minutely lacerate; corolla salverform, glabrous without, the tube 1.5–2.0 cm. long, about 0.3 cm. in diameter at the base, sharply constricted at the insertion of the stamens, the lobes obliquely obovate, shortly acuminate, 1.0–1.4 cm. long, reflexed or spreading widely; stamens inserted about midway within the corolla-tube, the anthers lanceolate-sagittate, 0.6–0.65 cm. long, sparsely puberulent dorsally; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.15 cm. long; nectaries usually somewhat concrescent at the base, equalling or somewhat surpassing the ovary; follicles relatively stout, continuous, falcate, 12–16 cm. long, glabrous; seeds about 1.5 cm. long, the pale tawny coma about 0.2 cm. long.

BRAZIL: PERNAMBUCO: data incomplete, *Gardner 1060* (Camb.); MINAS GERAES: Pico d'Itabira, 1843, *Glaussen 35* (MP, NY); RIO DE JANEIRO: Mage, date lacking,



Miers 4030 (BM, US); SÃO PAULO: Santos, April 1, 1875, *Mosen 3020* (S); Cubatão, alt. 0-50 m, March 2, 1929, *Smith 2087* (G, MBG); PARANA: Tacarehy, in fruticetis, Febr. 11, 1915, *Dusen 16684* (MBG, S); Paranagua, ad marginem silvulae, March, 1914, *Jonsson 2a* (S); Rio Cubatão, ad marginem silvae fluminalis, Dec. 28, 1911, *Dusen 13696* (S); Porto Dom Pedro II, in insula in fruticetis, Febr. 25, 1911, *Dusen 11449* (MBG, S); Tacarehy, in silva primaeva ad marg. regionis lit., March 18, 1914, *Jonsson 91a* (S, US).

Several color forms are known of this species, which has been cultivated in Europe as a greenhouse or "stove" ornamental since prior to 1835 when it was illustrated and discussed in Edwards' Botanical Register 20: *pl. 1664*. The various color forms were interpreted subspecifically by Mueller, and later raised to specific rank by Miers. The species having been neglected horticulturally in recent years, it has been impossible to obtain first-hand knowledge of the color variation; and since herbarium specimens retain little by which they may be recognized, it has been considered best to retain the integrity of the species.

3. *Temnadenia ornata* (Hoehne) Woodson, Ann. Mo. Bot. Gard. 19: 383. 1932.

*Echites ornata* Hoehne, Comm. Linh. Telegr. Estrat. Matto Grosso, Anexo 5, Bot. 6: 82. *pls. 120; 131, fig. 1*, 1915.

Stems relatively slender, glabrous; leaves opposite, shortly petiolate, oblong-lanceolate, apex abruptly acuminate, base obtuse, 8-12 cm. long, 3.5-4.5 cm. broad, glabrous, somewhat nitidulous above; petioles 0.4-0.5 cm. long; inflorescence repeatedly and rather irregularly di- or trichotomous, relatively lax, somewhat surpassing the subtending leaves, bearing 15-25 yellowish, crimson-flushed flowers, glabrous throughout; pedicels 1.0-1.2 cm. long; bracts lanceolate, 0.3-0.5 cm. long, somewhat foliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.3 cm. long, reflexed at the tips, slightly foliaceous, the squamellae deeply lacerate; corolla salverform, glabrous without, the tube 1.0-1.5 cm long, about 0.125 cm. in diameter at the base, somewhat dilating toward the orifice, the lobes obliquely obovate, 2.0-2.5 cm. long, acuminate, widely spreading or somewhat reflexed; stamens inserted about midway within the corolla-tube, the anthers 0.5 cm. long; carpels ovoid, about 0.125 cm. long,

glabrous; stigma 0.1 cm. long; nectaries separate, about half equalling the carpels; follicles unknown.

BRAZIL: MATTO GROSSO: Proecedencia Piruena, May, 1909, *Hoehne 1965* (B, isotype, MBG, photograph and analytical drawings).

4. *Temnadenia violacea* (Vell.) Miers, Apoc. So. Am. 208. 1878.

*Echites violacea* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 31. 1827; A. DC. in DC. Prodr. 8: 459. 1844; Stadelm. Flora 24<sup>1</sup>: Beibl. 34. 1841; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 158. pl. 50, fig. 3. 1860.

*Echites Maximiliana* Stadelm. loc. cit. 43. 1841.

*Echites Franciscea* A. DC. loc. cit. 452. 1844.

Stems relatively stout, densely hispidulous to glabrate; leaves opposite, petiolate, ovate-elliptic, acuminate, base obtuse to rounded, 7–10 cm. long, 3–6 cm. broad, firmly membranaceous, above densely and minutely bullate-hispidulous to glabrate, beneath densely puberulent; petioles 0.3–0.5 cm. long, puberulent; inflorescence somewhat surpassing the subtending leaves, softly puberulent without, bearing 4–9 congested, crimson-purple to deep rose-colored flowers; peduncle obscurely dichotomous to essentially simple; pedicels 1.0–1.2 cm. long, puberulent-papillate; bracts lanceolate, 0.5–0.8 cm. long, subfoliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.5–0.7 cm. long, irregularly puberulent without, the squamellae deeply lacerate; corolla infundibuliform, glabrous without, the proper-tube 1.5–1.7 cm. long, about 0.3 cm. in diameter at the base, slightly constricting toward the insertion of the stamens, the throat conical, 1.5–2.0 cm. long, about 0.8–1.0 cm. in diameter at the orifice, the lobes broadly and obliquely obovate, 1.5–2.0 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers 1 cm. long, minutely puberulent-papillate dorsally; ovary ovoid-oblongoid, about 0.4 cm. long; stigma 0.2 cm. long; nectaries essentially separate, about half equalling the ovary; follicles unknown.

BRAZIL: CEARA: Campo Grande, in carrascal, March 17, 1910, *Lofgren 282* (S); MINAS GERAES: ad Lagoa Santa, Jangada, in silva, date lacking, *Warming s.n.* (C); data incomplete, Aug.–April, 1840, *Claussen s.n.* (Camb.); RIO DE JANEIRO: ad Rio de Janeiro, June, 1866, *Engel s.n.* (C); SÃO PAULO: Santa Rita do Passa Quatro, Nov. 1, 1897, *Hemndorff 36* (S); PARANA: Itarare, ad marg. silvulae, March 19,

1915, *Dusen 16835* (S); Itarare, opp. Monengava, in campo cerrado, alt. 740 m., Jan. 26, 1915, *Dusen 16608* (MBG); inter Senges et Fabio Rego, ad marg. silvulae, alt. 770 m., Dec. 11, 1910, *Dusen 11038* (MBG, S, US).

## EXCLUDED SPECIES

*Temnadenia annularis* (L.f.) Miers, Apoc. So. Am. 216. 1878 (*Echites annularis* L.f. Suppl. 166. 1781) = **Prestonia annularis** (L.f.) G. Don, Gen. Hist. 4: 84. 1838.

*Temnadenia cordata* (A. DC.) Miers, Apoc. So. Am. 212. 1878 (*Echites cordata* A. DC. in DC. Prodr. 8: 451. 1844) = **Mandevilla oaxacana** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882 (*Echites Oaxacana* A. DC. loc. cit. 451. 1844).

*Temnadenia corrugulata* Miers, Apoc. So. Am. 215. 1878 = **Prestonia solanifolia** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 23: 282. 1936.

*Temnadenia glaucescens* (Mart. & Gal.) Miers, Apoc. So. Am. 214. 1878 (*Echites glaucescens* Mart. & Gal. Acad. Roy. Brux. 11<sup>1</sup>: 358. 1844) = **Mandevilla oaxacana** (A. DC.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882 (*Echites Oaxacana* A. DC. in DC. Prodr. 8: 451. 1844).

*Temnadenia lasiocarpa* Miers, Apoc. So. Am. 210. 1878 (*Echites lasiocarpa* A. DC. in DC. Prodr. 8: 463. 1844) = **Mandevilla lasiocarpa** (A. DC.) Malme, Bihang till K. Sv. Vet. Akad. Handl. Afd. III. 24<sup>10</sup>: 25. 1899.

*Temnadenia leptoloba* (Stadelm.) Miers, Apoc. So. Am. 211. 1878 (*Echites leptoloba* Stadelm. Flora 24<sup>1</sup>: Beibl. 15. 1841) = **Prestonia agglutinata** (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931 (*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760).

*Temnadenia Lobbiana* (A. DC.) Miers, Apoc. So. Am. 209. 1878 (*Echites lasiocarpa* A. DC. γ *Lobbiana* A. DC. in DC. Prodr. 8: 464. 1844) = **Mandevilla lasiocarpa** (A. DC.) Malme, Bihang till K. Sv. Vet. Akad. Handl. Afd. III. 24<sup>10</sup>: 25. 1899 (*Echites lasiocarpa* A. DC. loc. cit. 463. 1844).

*Temnadenia palustris* (Muell.-Arg.) Miers, Apoc. So. Am. 213. 1878 (*Amblyanthera palustris* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 145. 1860) = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hir-*

*suta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792, not R. & P.).

*Temnadenia parviflora* (Benth.) Miers, Apoc. So. Am. 215. 1878 (*Haemadictyon parviflorum* Benth. Pl. Hartw. 355. 1857) = **Prestonia parviflora** Benth. in Benth. & Hook. Gen. Pl. 2: 709. 1873.

*Temnadenia quinquangularis* (Jacq.) Miers, Apoc. So. Am. 217. 1878 (*Echites quinquangularis* Jacq. Enum. Pl. Carib. 13. 1760) = **Prestonia quinquangularis** (Jacq.) Spreng. Syst. 1: 637. 1825.

*Temnadenia Riedelii* (Muell.-Arg.) Miers, Apoc. So. Am. 216. 1878 (*Haemadictyon Riedelii* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 170. 1860) = **Prestonia Riedelii** (Muell.-Arg.) Mgf. in Fedde, Rep. Spec. Nov. 20: 26. 1924.

*Temnadenia secundiflora* (A. DC.) Miers, Apoc. So. Am. 211. 1878 (*Echites secundiflora* A. DC. in DC. Prodr. 8: 457. 1844) = **Mandevilla subsagittata** (R. & P.) Woodson, Ann. Mo. Bot. Gard. 19: 69. 1932 (*Echites subsagittata* R. & P. Fl. Peruv. 2: 19. 1799).

*Temnadenia semidigyna* (Berg) Miers, Apoc. So. Am. 213. 1878 (*Echites semidigyna* Berg, Abh. Zeeuwisch Gen. Wetens. 3: 583. 1773). This appears to be an unidentifiable species of *Tabernaemontana*.

*Temnadenia solanifolia* (Muell.-Arg.) Miers, Apoc. So. Am. 214. 1878 (*Haemadictyon* (?) *solanifolium* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 171. pl. 49. 1860) = **Prestonia solanifolia** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 23: 282. 1936.

*Temnadenia tenuicula* Miers, Apoc. So. Am. 216. 1878 = **Prestonia solanifolia** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 23: 282. 1936 (*Haemadictyon* (?) *solanifolium* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 171. pl. 49. 1860).

*Temnadenia tomentosa* (Vahl) Miers, Apoc. So. Am. 213. 1878 (*Echites tomentosa* Vahl, Symb. Bot. 3: 44. 1794) = **Mandevilla hirsuta** (A. Rich.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895 (*Echites hirsuta* A. Rich. Actes Soc. Hist. Nat. Paris 1: 107. 1792, not R. & P.).

*Temnadenia xanthostoma* (Stadelm.) Miers, Apoc. So. Am.

212. 1878 (*Echites xanthostoma* Stadelm. Flora 24<sup>1</sup>: Beibl. 55. 1841) = *Mandevilla coccinea* (Hook. & Arn.) Woodson, Ann. Mo. Bot. Gard. 20: 734. 1933 (*Echites coccinea* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834).

## XXII. FERNALDIA Woodson

*Fernaldia* Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

Lactescent, fruticose or suffruticose lianas. Stems volubile, terete; branches alternate, or opposite below. Leaves opposite, petiolate, entire, penninerved, eglandular; petioles subtended by several minute, pectinate, adaxial stipular appendages. Inflorescence lateral, alternate, simply scorpioid, bearing several rather showy, white flowers. Calyx 5-parted, the lobes equal to subequal, cleft nearly to the receptacle, imbricated, scarious or only very slightly foliaceous, bearing solitary opposite squamellae within at the base. Corolla infundibuliform, slightly gibbous to essentially straight, the tube exappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute, more or less arachnoid-villous within. Stamens 5, included, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged obtusely 2-auriculate, peltate connective; pollen granular. Carpels 2, united at the apex by a slender stylar shaft surmounted by the fusiform-capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries concrescent, unequally 4-lobed. Follicles 2, apocarpous, terete, acuminate, dehiscing along the ventral suture, containing many dry, truncate, apically comose seeds.

Type species: *Fernaldia pandurata* (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

### KEY TO THE SPECIES

- a. Corolla glabrous without, or essentially so, or the lobes occasionally ciliate without, the proper-tube 2.0–2.2 cm. long, about 0.15 cm. in diameter at the base, somewhat gibbous at the insertion of the stamens, the throat broadly campanulate-conical, 0.9–1.2 cm. long.....1. *F. pandurata*
- aa. Corolla generally pilosulose without, the proper-tube 1.8–2.0 cm. long, about 0.3 cm. in diameter at the base, scarcely gibbous, the throat rather narrowly conical, 1.6–1.8 cm. long.....2. *F. brachypharynx*

1. *Fernaldia pandurata* (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 48. 1932.

*Echites pandurata* A. DC. in DC. Prodr. 8: 458. 1844.

*Urechites Karwinskii* Muell.-Arg. Linnaea 30: 440. 1860;

Miers, Apoc. So. Am. 125. 1878.

*Amblyanthera* ? *pandurata* (A. DC.) Muell.-Arg. loc. cit. 448. 1860.

*Angadenia pandurata* (A. DC.) Miers, loc. cit. 182. 1878.

*Mandevilla velutina* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 171. 1895, not Woodson.

*Mandevillea potosina* T. S. Brandg. Univ. Calif. Publ. Bot. 4: 276. 1912.

*Echites pinguiifolia* Standl. Field Mus. Publ. Bot. 8: 35. 1930.

#### Plate 5.

Stems relatively slender, densely puberulent to essentially glabrate; leaves opposite, oblong-elliptic to broadly ovate, apex shortly acuminate, the lower usually broadly cordate, the upper merely obtuse to subtruncate at the base, 4–13 cm. long, 1.5–3.0 cm. broad, membranaceous, either surface densely puberulent to velutinous, or the upper essentially glabrate; petioles 1–2 cm. long, minutely puberulent to essentially glabrate; inflorescence lateral, simply scorpioid, bearing 6–18 rather showy, white to pale greenish-yellow flowers, the peduncle usually about half equalling the subtending leaves, minutely puberulent; pedicels 0.4–0.6 cm. long, minutely puberulent, congested toward the upper half of the peduncle; bracts ovate, acute to acuminate, scarious or only slightly foliaceous, 0.1–0.2 cm. long; calyxlobes ovate, acute to obtuse, 0.2–0.3 cm. long, minutely puberulent to puberulent-papillate without, the squamellae very minutely crenulate or erose; corolla infundibuliform, essentially glabrous without, or the lobes more or less ciliate, the proper-tube 2.0–2.2 cm. long, about 0.15 cm. in diameter at the base, somewhat gibbous or arcuate at the insertion of the stamens, the throat broadly campanulate-conical, 0.9–1.2 cm. long, 0.7–0.9 cm. in diameter at the orifice, the lobes obliquely obovate, acute to acuminate, 1.0–1.3 cm. long, densely arachnoid-villous

at the base within, the margins occasionally ciliate, patulous; stamens inserted at the base of the corolla-throat, the anthers broadly elliptic-sagittate, shortly and rather obtusely auriculate, 0.6–0.65 cm. long, glabrous; ovary ovoid-oblongoid, about 0.2 cm. long, glabrous; stigma 0.2 cm. long; nectaries unequally 4-lobed, only slightly fleshy, about half equalling the ovary; mature follicles unknown.

MEXICO: TAMAULIPAS: El Rosario, vicinity of Marmolejo, alt. 2100 ft., Aug. 10, 1930, *Bartlett 10873* (US); SAN LUIS POTOSI: Rascon, Aug., 1911, *Purpus 5408* (MBG, NY); VERA CRUZ: Baños del Carrizal, Aug., 1912, *Purpus 6293* (MBG, US); GUERRERO: Acapulco and vicinity, Oct., 1894–March, 1895, *Palmer 259* (G, US); OAXACA: Cafetal Las Pitas, alt. 400 m., Oct. 10, 1917, *Reko 3511* (US); YUCATAN: Izamal, 1895, *Gaumer 815* (MBG).

EL SALVADOR: San Salvador, alt. 657 m., date lacking, *Laboratorio Químico 2* (MBG, US); cultivated, vicinity of San Salvador, alt. 650–850 m., March 30–April 24, 1922, *Standley 23543* (NY, US).

Also reported from Costa Rica. The lowermost leaves are said to be more or less pandurate in outline. The popular name of the species is reported as “loroco,” or “floroco,” and the flowers are said by Standley to be used as a flavoring for rice. Notes on the label of the specimen from the chemical laboratory of the argicultural department of El Salvador state: “Flores en la estacion lluviosa. Flores comestibles despues de cociamiento. Muy apreciadas por su olor y sabor en la comida. Abunda en los mercados.”

**2. *Fernaldia brachypharynx* Woodson, Ann. Mo. Bot. Gard. 19: 380. 1932.**

Stems relatively slender, minutely puberulent to glabrate when fully mature; leaves opposite, petiolate, broadly ovate, shortly and abruptly acuminate, base broadly rounded, 7–10 cm. long, 5–7 cm. broad, membranaceous, above densely hispidulous to very minutely puberulent-papillate, beneath velutinous to rather minutely and sparsely puberulent; petioles 0.9–2.0 cm. long, pilosulose; inflorescence lateral, simply scorpioid, the peduncle much shorter than the subtending leaves, minutely puberulent; pedicels 0.4–0.5 cm. long, minutely puberulent, congested toward the upper half of the peduncle; bracts ovate, 0.1–0.2 cm. long; calyx-lobes ovate, acuminate, 0.2–0.3

cm. long, minutely and sparsely pilosulose without, the squamellae deltoid, minutely crenulate; corolla infundibuliform, generally pilosulose without, the proper-tube 1.8–2.0 cm. long, about 0.3 cm. in diameter at the base, the throat rather narrowly conical, 1.6–1.8 cm. long, about 0.7 cm. in diameter at the orifice, the lobes obliquely obovate, acuminate, 1.2–1.4 cm. long, arachnoid-villous at the base within, patulous; stamens inserted at the base of the corolla-throat, the anthers elliptic-sagittate, shortly and rather obtusely auriculate, 0.6 cm. long, glabrous; ovary ovoid-oblongoid, about 0.15 cm. long, glabrous; stigma 0.2 cm. long; nectary irregularly 4-lobed, only slightly fleshy, about half equalling the ovary; follicles unknown.

GUATEMALA: ESCUINTLA: along the road from Escuintla to the port of San Jose de Guatemala, Aug. 23, 1860, *Hayes s.n.* (G, TYPE, MBG, photograph and analytical drawings); Villa Nueva, Sept., 1914, *Tejada 249* (US).

### XXIII. ASKETANTHERA Woodson

*Asketanthera* Woodson, Ann. Mo. Bot. Gard. 19: 46. 1932.

*Echites* of authors, in part, not P. Br.

Lactescent, suffruticose or suffrutescent lianas. Stems volatile, terete; branches mostly opposite below, becoming alternate above. Leaves opposite, petiolate, entire, penninerved, eglandular; petioles subtended by several minute, pectinate, adaxial, stipular appendages. Inflorescence lateral, alternate, simply scorpioid, bearing several showy, pedicellate flowers subtended by conspicuously foliaceous bracts. Calyx 5-parted, the lobes subequal, cleft nearly to the receptacle, imbricated, strikingly foliaceous, bearing solitary, opposite squamellae within at the base. Corolla salverform, the tube straight, ex-appendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, included, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, sagittate, narrowly 2-auriculate connective; pollen granular. Carpels 2, united at the apex by a slender stylar shaft surmounted by the fusiform-capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta.



Nectaries 5, separate or somewhat concrescent at the base. Follicles 2, apocarpous, terete, dehiscent along the ventral suture, containing many dry, rostrate, apically comose seeds.

Type species: *Asketanthera calycosa* (A. Rich.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

#### KEY TO THE SPECIES

- a. Stamens inserted about midway within the corolla-tube, the anthers barely included; plants of Cuba.....1. *A. calycosa*
- aa. Stamens inserted near the base of the corolla-tube, the anthers deeply included; species of Hispaniola.
  - b. Corolla 2-5 cm. long; inflorescence 8-20-flowered.
    - c. Corolla 2.0-2.5 cm. long, the tube somewhat shorter than the calyx-lobes, essentially glabrous without.....2. *A. Picardae*
    - cc. Corolla 4-5 cm. long, the tube conspicuously surpassing the calyx-lobes, hispidulous without.....3. *A. dolichopetala*
  - bb. Corolla 13-16 cm. long; inflorescence 2-8-flowered.....4. *A. Ekmaniana*

1. *Asketanthera calycosa* (A. Rich.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Echites calycosa* A. Rich. in Sagra, Hist. Cuba 11: 94. 1850.

*Rhodocalyx calycosus* (A. Rich.) Miers, Apoc. So. Am. 140. 1878.

*Echites Rugeliana* Urb. Symb. Ant. 5: 465. 1908.

#### Plate 6.

Stems relatively stout, densely ferruginous-hispidulous to glabrate. Leaves opposite, petiolate, broadly ovate-elliptic, apex acuminate, base obtuse to rounded, 8-15 cm. long, 5-9 cm. broad, membranaceous, above minutely strigillose to glabrate, beneath densely puberulent-pilosulose; petioles 0.7-1.0 cm. long, densely puberulent-pilosulose; inflorescence corymbose, bearing 5-12 congested, pale greenish-white or yellowish flowers; peduncle somewhat shorter than the subtending leaves, hispidulous; pedicels 1.0-1.5 cm. long, densely hispidulous; bracts lanceolate, conspicuously foliaceous, 1.2-2.0 cm. long; calyx-lobes elliptic-lanceolate, acuminate, 1-2 cm. long, conspicuously foliaceous, rather sparsely pilose, the squamellae deltoid, truncate, essentially entire; corolla salverform, rather sparsely pilosulose without, the tube 1.0-1.3 cm. long, about 0.2

cm. in diameter at the base, the lobes obliquely elliptic-oblongate, acute, 3.0–4.5 cm. long, patulous; stamens inserted about midway within the corolla-tube, the anthers narrowly lanceolate-sagittate, 0.8 cm. long, glabrous; ovary ovoid, about 0.3 cm. long, glabrous; stigma 0.2 cm. long; nectaries about half equalling the ovary; follicles relatively stout, continuous, acuminate, 25–30 cm. long, densely ferruginous-hispid; seeds 1.6–1.9 cm. long, the pale tawny coma 3.0–3.5 cm. long.

CUBA: PINAR DEL RIO: Sierra de los Organos, grupo del Rosario, valley of Rio Santa Cruz, March 31, 1923, *Ekman 16390* (S); HABANA: Sierra Anafe, in the part of the Sierra called "Loma Esperon," in one of the deep clefts, July 11, 1921, *Ekman 13037* (S); ORIENTE: Sierra de Nipe, in marracales at Rio Barigua, Sept. 30, 1922, *Ekman 15311* (S); Baracoa, in vall. flumin. Rio Macaguanigua, Jan. 19, 1915, *Ekman 4340* (S); Sierra Maestra, El Peru, rocky gulch of Arroyo del Peru, Aug. 8, 1922, *Ekman 16409* (B, S); Sierra de Nipe, "El Taller," ad Rio Piloto, Febr. 18, 1918, *Ekman 9051* (S); Bayamon, alt. 500 m., Febr., 1889, *Eggers 4707* (B, US); data incomplete, *Wright 1377* (B, Bx, K, MBG); MATANZAS [?]: ad fluv. San Juan, date lacking, *Eugel 397* (B).

*Echites Rugeliana* Urb. differs from *E. calycosa* A. Rich. only in the somewhat larger calyx and corolla, a character which is rendered insignificant by great variability. Extreme specimens of either are found on the same herbarium sheet of *Wright 1377* in the herbarium of the Missouri Botanical Garden.

## 2. *Asketanthera Picardae* (Urb.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Echites Picardae* Urb. Symb. Ant. 5: 466. 1908.

Stems relatively slender, minutely ferruginous-puberulent to glabrate; leaves opposite, petiolate, ovate-elliptic, apex acuminate, base obtuse, 8–15 cm. long, 3–9 cm. broad, delicately membranaceous, above minutely strigillose to glabrate, beneath very minutely puberulent to glabrate; petioles 0.7–1.0 cm. long, minutely puberulent; inflorescence corymbose, bearing 8–20 greenish-yellow flowers; peduncle about half equalling the subtending leaves, minutely ferruginous-puberulent; pedicels 0.5–0.8 cm. long, minutely ferruginous-puberulent; bracts elliptic-lanceolate, acute to acuminate, 1.5–2.0 cm. long, conspicuously foliaceous; corolla salverform, essentially glabrous without, the tube 1.2–1.5 cm. long, about 0.1 cm. in diameter at

the base, the lobes obliquely obovate-oblong, acute, 0.8–1.0 cm. long, patulous; stamens inserted near the base of the corolla-tube, the anthers narrowly lanceolate, sagittate, 0.7 cm. long, glabrous; ovary oblongoid, about 0.2 cm. long, glabrous; nectaries about half equalling the ovary; follicles continuous, acuminate, 30–45 cm. long, glabrous; seeds 1.7 cm. long, the pale tawny coma 4 cm. long.

**HISPANIOLA: HAITI:** in montibus prope Pétionville, alt. 400 m., July 17, 1891, *Picarda 804* (B); Pte. Rivière des Nippes, hillside at Bellevue, alt. 500 m., July 16, 1927, *Ekman 8590* (B, S, US); Presqu'île de Nord-ouest, montagnes de Terre-neuve, Gros Morne, limestone precipices, alt. 400 m., Oct. 10, 1925, *Ekman 5053* (B, S); Massif de la Hotte, eastern group, Aquin, La Colline, in Morne des Abricots, alt. 500 m., Nov. 9, 1926, *Ekman 7191* (B); Massif de la Hotte, eastern group, Miragoane, limestone cliffs south of Étang-Miragoane, July 28, 1926, *Ekman 6536* (B, S); Presqu'île du Nord-ouest, Les Gonaïves, between Bassin and Mémé, alt. 350 m., Dec. 24, 1927, *Ekman 9460* (B, S); Basse Vallée de Siburon, Sept. 2, 1910, *Christ 2279* (B); prope Bel Endroit, in fruticosis densis, Aug. 9, 1917, *Ekman 659* (B, S).

**3. *Asketanthera dolichopetala* (Urb.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.**

*Echites dolichopetala* Urb. Symb. Ant. 7: 335. 1912.

Stems relatively stout, densely and minutely ferruginous-hispidulous to glabrate; leaves opposite, petiolate, ovate-elliptic, apex abruptly acuminate, base rather abruptly obtuse, 6–10 cm. long, 4–6 cm. broad, above densely strigillose-hispidulous, beneath densely and minutely pilosulose; petioles 1.5–2.0 cm. long, densely and minutely hispidulous; inflorescence corymbose, bearing 8–12 congested greenish cream-colored flowers; peduncle about equalling or somewhat surpassing the subtending leaves, minutely and densely ferruginous-puberulent; pedicels 0.5–0.8 cm. long, minutely ferruginous-puberulent; bracts broadly lanceolate, 1.0–1.5 cm. long, conspicuously foliaceous; calyx-lobes broadly lanceolate, acuminate, 1.2–1.7 cm. long, conspicuously foliaceous, pilosulose, the squamellae deltoid, deeply lacerate; corolla salverform, densely ferruginous-hispidulous without, the tube 1.5–2.2 cm. long, about 0.2 cm. in diameter at the base, the lobes obliquely obovate-lanceolate, acute, 2.5–2.7 cm. long, patulous; stamens inserted near the base of the corolla-tube, the anthers broadly elliptic-

sagittate, 0.7 cm. long, glabrous; ovary ovoid, about 0.2 cm. long; nectaries somewhat shorter than the ovary; follicles unknown.

HISPANIOLA: SANTO DOMINGO: Barahona, in via ad El Marviel, alt. 100 m., July, 1910, *Fuertes 453* (B, BM, K, MBG, S); data incomplete, *Martin s.n.* (DL).

A species offering a striking similarity in superficial aspect to *A. calycosa* of Cuba, but differing in the deeper insertion of the stamens, the harsher indument, and the deeply lacerate squamellae.

4. *Asketanthera Ekmaniana* Woodson, nom. nov.

*Echites longiflora* Ekm. & Helwig, Arkiv f. Bot. **22A**<sup>10</sup>: 45. 1929, not Desf.

*Asketanthera longiflora* (Ekm. & Helwig) Woodson, Ann. Mo. Bot. Gard. **19**: 47. 1932.

Stems relatively slender, very minutely puberulent to glabrate; leaves opposite, petiolate, ovate to broadly elliptic-lanceolate, apex acuminate, base obtuse, 9–14 cm. long, 4–8 cm. broad, delicately membranaceous, above essentially glabrous, beneath very minutely puberulent-papillate to glabrate; petioles 0.5–0.8 cm. long, minutely puberulent-papillate; inflorescence corymbose, bearing 2–8 very showy, greenish-white or cream-colored flowers; peduncle about half equalling the subtending leaves, glabrate; pedicels 1.0–1.2 cm. long, essentially glabrous; bracts broadly elliptic-lanceolate, 1.5–2.0 cm. long, conspicuously foliaceous; calyx-lobes broadly elliptic-lanceolate, acuminate, 2.0–2.5 cm. long, conspicuously foliaceous; corolla salverform, glabrous without, the tube 7–8 cm. long, about 0.2 cm. in diameter at the base, the lobes obliquely elliptic-lanceolate, 6–8 cm. long, patulous; stamens inserted near the base of the corolla-tube, the anthers narrowly oblong-sagittate, 0.8–1.0 cm. long, glabrous; ovary oblongoid, about 0.3 cm. long, glabrous; nectaries somewhat concrescent at the base, about one-third equalling the ovary; mature follicles unknown.

HISPANIOLA: HAITI: eastern La Hotte, Chapelle Mont Carmel, in a gulch, Nov. 8, 1924, *Ekman 2426* (S); Massif de la Hotte, eastern group, Pte. Gonave, near Chap. St.-Michel, deep limestone hill, date lacking, *Ekman 6598* (B, S); SANTO

DOMINGO: Cordillera de Barahona, Sierra de los Comisarios, between Banane and Gros Figuier, limestone, alt. 500 m., Aug. 28, 1926, *Ekman 6763* (B, S).

A most remarkable plant, which seems to be a fairly free bloomer, and certainly appears to be a worthy subject for cultivation in greenhouses.

#### XXIV. MACROPHARYNX Rusby

**Macropharynx** Rusby, Mem. N. Y. Bot. Gard. 7: 327. *pl.* 6. 1927.

Lactescent, fruticose lianas. Stems volubile, terete; branches opposite. Leaves opposite, petiolate, entire, penninerved, eglandular; petioles subtended by several minute, adaxial, pectinate, stipular appendages. Inflorescence lateral, opposite or infrequently alternate, an extremely condensed, subumbellate cincinnus, conspicuously bracteate, bearing few to several showy, greenish-white flowers. Calyx 7-9-parted (or 5-parted ?), the lobes somewhat unequal, more or less foliaceous, imbricated, cleft nearly to the receptacle, bearing within at the base a solitary, opposite squamella. Corolla infundibuliform (or salverform ?), the tube straight, exappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens, 5, included, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, acutely 2-auriculate connective; pollen granular. Carpels 2, united at the apex by a slender stylar shaft surmounted by the fusiform stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or somewhat concrescent at the base. Follicles 2, apocarpous, terete, dehiscing along the ventral suture, containing many dry, comose seeds.

Type species: *Macropharynx spectabilis* (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

#### KEY TO THE SPECIES

- a. Corolla infundibuliform to subsalverform; calyx-lobes 7-9, immediately subtended by similar bracts.....1. *M. spectabilis*
- aa. Corolla salverform; calyx-lobes 5, not immediately subtended by bracts....  
.....2. *M. anomala*

1. **Macropharynx spectabilis** (Stadelm.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites spectabilis* Stadelm. Flora 24<sup>1</sup>: Beibl. 44. 1841;  
A. DC. in DC. Prodr. 8: 462. 1844; Muell.-Arg. in Mart.  
Fl. Bras. 6<sup>1</sup>: 153. 1860.

*Elytropus spectabilis* (Stadelm.) Miers, Apoc. So. Am.  
116. 1878.

*Macropharynx fistulosa* Rusby, Mem. N. Y. Bot. Gard. 7:  
329. pl. 6. 1927.

Stems stout, densely and minutely ferruginous-tomentulose when young, eventually becoming glabrate; leaves opposite, petiolate, broadly ovate, apex very shortly and abruptly acuminate, base rounded to broadly and rather obscurely cordate, 9–30 cm. long, 5–17 cm. broad, firmly membranaceous to subcoriaceous, above minutely ferruginous-puberulent when young, glabrate and rather lustrous when fully mature, beneath minutely ferruginous-pilosulose to glabrate; petioles 3–5 cm. long, indument as upon the stem; inflorescence lateral, usually opposite, subumbellate, bearing 1–5 showy, greenish-white flowers; peduncle extremely condensed, about half equalling the subtending petioles, minutely ferruginous-puberulent; bracts linear, 0.4–1.2 cm. long, subfoliaceous, usually ferruginous-pilosulose; calyx-lobes 7–9, linear, long-acuminate, 0.9–1.3 cm. long, ferruginous-puberulent or -pilosulose without, subfoliaceous, the squamellae minutely lacerate; corolla infundibuliform or subsalverform, glabrous without, or essentially so, the proper-tube 0.7–1.0 cm. long, about 0.2–0.3 cm. in diameter at the base, the throat subtubular, 1.3–4.0 cm. long, about 0.4–0.8 cm. in diameter at the orifice, the lobes obliquely obovate, 1.2–1.7 cm. long, patulous; stamens inserted at the base of the corolla-throat, the anthers narrowly sagittate, 0.9–1.0 cm. long, glabrous; ovary ovoid-oblongoid, about 0.3 cm. long, minutely puberulent-papillate to essentially glabrous; stigma 0.2 cm. long; nectaries equalling to somewhat surpassing the ovary; follicles relatively stout, 22–25 cm. long, ferruginous-hispidulous when young, eventually glabrate; seeds unknown.

BRAZIL: PARA: Belem, ad marginem silvae prope lacum Catu, Jan. 1, 1926, Ducke 21536 (B, US); AMAZONAS: in silvis ad Manacuru, ditionis Japurensis, 1920,

*Martius s.n.* (B, TYPE); schlingend in den Hugelwaldchen von Porongo bei Santa Cruz, Jan. 1911, *Hersog 1513* (B).

PERU: LORETO: Stromgebiet des Maranon von Jquitos aufwrts bis zur Santiagomndung am Pongo de Mansericho, June 23, 1924, *Tessmann 3607* (B); Iquitos, woods, alt. about 100 m., Aug. 3-11, 1929, *Killip & Smith 27193* (MBG, NY, US); Mishuyacu, near Iquitos, forest, alt. 100 m., Oct.-Nov., 1929, *Klug 541* (NY, US).

BOLIVIA: BENI: Rurrenabaque, alt. 1000 ft., Dec. 1, 1921, *Cardenas 1894* (K, NY, US); LA PAZ: San Carlos bei Sarompiuni, alt. 600 m., Dec. 21, 1926, *Buchtien 1743* (NY); SANTA CRUZ: Rio Surutu, Prov. Sara, Dec. 27, 1924, *Steinbach 6813* (B, K, MBG); Banados del Piray, Buenaventura, alt. 450 m., May, 1915, *Lillo 1314* (B); Pamparegion de Buenavista, Prov. del Zara, alt. 400 m., Dec. 23, 1916, *Lillo 3200* (B).

Steinbach reports "No hace randaes, porque ramifera poco." It is a great temptation to segregate the specimens cited above into two, or perhaps three species or varieties based upon discrepancies in the size of the corolla, and on the indument of the inflorescence. The flora of the region from which they come is so inadequately understood, however, that it is believed more practical to preserve the integrity of the species for the present. In the herbarium at Berlin-Dahlem there is a specimen, supposedly of this same species, bearing the data "in silvis pr. Paramaribo," without date, collected by Kegel (174). The data has appeared too dubious to incorporate with the better substantiated range records in the Amazon valley.

**2. *Macropharynx* [?] *anomala*** Woodson, Ann. Mo. Bot. Gard. 21: 614. 1934.

Stems relatively slender, minutely and densely ferruginous-tomentulose to glabrate; leaves opposite, petiolate, broadly ovate, apex shortly and narrowly subcaudate-acuminate, base broadly obtuse to rounded, frequently rather obscurely cordate, 10-18 cm. long, 5-9 cm. broad, membranaceous, above rather irregularly ferruginous-puberulent to -papillate, beneath densely and very minutely ferruginous-tomentulose; petioles 2.5-3.0 cm. long, minutely ferruginous-tomentulose; inflorescence lateral, opposite, subumbellate-fasciculate, relatively few-flowered; peduncle minutely ferruginous-tomentulose, somewhat shorter than the subtending petioles; pedicels 0.15-0.2 cm. long, minutely ferruginous-tomentulose; bracts linear, 1.0-1.4 cm. long, somewhat foliaceous, minutely pilosu-

lose to puberulent-papillate; calyx-lobes 5, narrowly elliptic-lanceolate, 1.7–1.8 cm. long, somewhat foliaceous, minutely puberulent-papillate, the squamellae deltoid, minutely denticulate; corolla salverform, minutely puberulent-papillate without, the tube (in well-formed buds) 1.4–1.6 cm. long, about 0.2 cm. in diameter at the base, somewhat inflated at the insertion of the stamens thence gradually constricting toward the orifice, the lobes rather narrowly ovate-dolabriform, acuminate, 0.9–1.0 cm. long, patulous; stamens inserted near the base of the corolla-tube, the anthers included, narrowly sagittate, 0.7–0.72 cm. long, minutely papillate to essentially glabrous dorsally; ovary oblongoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries slightly surpassing the ovary; follicles unknown.

ECUADOR: in silv. tropic. fl. Pilaton, Oct., 1902, *Sodiro 107/16* (B, TYPE, MBG, photograph and analytical drawings).

A discussion of reasons for and against relegating this plant to *Macropharynx* will be found at the place of original publication.

## XXV. THENARDIA HBK.

*Thenardia* HBK. Nov. Gen. 3: 209. 1819; A. DC. in DC. Prodr. 8: 425. 1844; Benth. & Hook. Gen. Pl. 2: 710. 1876; Miers, Apoc. So. Am. 242. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 187. 1895, not Sesse & Mociño.

Lactescent, suffruticose or suffrutescent lianas. Stems terete; branches alternate, or occasionally opposite, particularly below. Leaves opposite, petiolate, entire, penninerved, eglandular, the petioles subtended by a solitary, adaxial, stipular appendage. Inflorescence a lateral, alternate, pedunculate, trichotomous, umbellate cyme, the ultimate branches extremely compressed, inconspicuously bracteate. Calyx 5-parted, the lobes equal or essentially so, cleft nearly to the receptacle imbricated, subtended by solitary, opposite squamellae. Corolla rotate to shortly salverform, the tube straight, exappendiculate within, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and ag-



glutinated to the stigma, consisting of 2 parallel sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective, widely exerted; filaments connate above; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the fusiform-capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, essentially separate, or somewhat conrescent at the base. Follicles 2, apocarpous, terete, dehiscent along the ventral suture, containing many dry, apically comose seeds (fide A. de Candolle).

Type species: *Thenardia floribunda* HBK. Nov. Gen. 3: 210. pl. 240. 1819.

#### KEY TO THE SPECIES

- a. Corolla relatively large and showy, the limb 2.0–2.8 cm. in diameter, the tube not sharply constricted at the insertion of the stamens.
  - b. Corolla shortly salverform, the tube 0.5–0.6 cm. long, the lobes 0.7–0.8 cm. long.....1. *Th. tubulifera*
  - bb. Corolla rotate, the tube 0.2–0.35 cm. long, the lobes 1.0–1.3 cm. long.....2. *Th. floribunda*
- aa. Corolla relatively small, the limb 1.2–1.5 cm. in diameter, the tube sharply constricted at the insertion of the stamens.
  - b. Corolla-lobes obtuse; squamellae narrowly oblong-trigonal, entire; nectaries about half equalling the ovary.....3. *Th. gonoloboides*
  - bb. Corolla-lobes acute; squamellae broadly oblong-dentiform, minutely erose; nectaries equalling or slightly surpassing the ovary.....4. *Th. Galeottiana*

1. *Thenardia tubulifera* Woodson, Ann. Mo. Bot. Gard. 19: 381. 1932.

Stems relatively slender, glabrous; leaves opposite, shortly petiolate, elliptic-lanceolate, apex subcaudate-acuminate, base obtuse, 4–9 cm. long, 1.5–3.0 cm. broad, membranaceous, glabrous above, sparsely pilosulose along the midrib and veins beneath; petioles 0.5–1.0 cm. long, sparsely pilosulose to glabrate; inflorescence equalling or somewhat surpassing the leaves, multiflorous; primary peduncle 2.5–3.0 cm. long, the secondary 0.5–0.8 cm. long; pedicels 2.5–2.7 cm. long, puberulent-papillate to essentially glabrous; bracts lanceolate, about 0.1–0.2 cm. long; calyx-lobes ovate-lanceolate, acuminate, 0.2–0.3 cm. long, essentially glabrous without, the squamellae deltiform, es-

sentially entire; corolla shortly salverform, glabrous without, the tube broadly cylindrical, 0.5–0.6 cm. long, about 0.2 cm. in diameter at the base, about 0.3 cm. in diameter at the orifice, slightly and gradually constricted somewhat above midway at the insertion of the stamens, the lobes obliquely obovate-orbicular, minutely apiculate, 0.7–0.8 cm. long, spreading; stamens barely exerted, the anthers 0.7–0.8 cm. long, the filaments 0.35–0.4 cm. long, minutely puberulent-papillate above; ovary ovoid, about 0.15 cm. long, glabrous; nectaries somewhat shorter than the ovary, essentially separate; stigma 0.125 cm. long; follicles unknown.

MEXICO: JALISCO: data incomplete, *Diquet s.n.* (NY, TYPE, US, MBG, photograph and analytical drawings); Tonila, alt. 1000 m., Sept., 1923, *Reko 4823* (US).

Reko reports his specimen as bearing pink, fragrant flowers, which evidently applies to the following species as well:

2. *Thenardia floribunda* HBK. Nov. Gen. 3: 210. *pl.* 240. 1819; A. DC. in DC. Prodr. 8: 425. 1844; Miers, Apoc. So. Am. 242. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895.

*Thenardia ? suaveolens* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 359. 1844.

Stems relatively slender, glabrous; leaves opposite, or rarely ternate, petiolate, oblong-elliptic, apex acutely subcaudate-acuminate, base obtuse, 5.5–13.0 cm. long, 2–5 cm. broad, delicately membranaceous, wholly glabrous or merely sparsely pilosulose at the base of the midrib beneath; petioles 0.8–1.5 cm. long, glabrous; inflorescence about equalling or somewhat surpassing the subtending leaves, multiflorous; primary peduncle 2.5–8.0 cm. long, essentially glabrous, the secondary 0.4–1.0 cm. long, minutely and sparsely pilosulose; pedicels 2.0–2.2 cm. long, essentially glabrous; bracts lanceolate, 0.05–0.1 cm. long; calyx-lobes ovate-lanceolate, acuminate, 0.25–0.3 cm. long, minutely papillate without, the squamellae deltiform, minutely erose; corolla rotate, glabrous or very indefinitely papillate without, the tube 0.2–0.35 cm. long, about 0.15 cm. in diameter at the base and 0.35–0.4 cm. in diameter at the orifice, barely

constricted just below the insertion of the stamens, the lobes obliquely obovate-dolabriform, subcaudate-acuminate, 1.1–1.3 cm. long, spreading; stamens widely exserted, the anthers 0.6–0.7 cm. long, the filaments 0.5–0.6 cm. long, minutely puberulent-papillate above; ovary ovoid, about 0.1 cm. long, glabrous; nectaries essentially separate, somewhat shorter than the ovary; stigma 0.15 cm. long; follicles unknown.

MEXICO: MORELOS: barranca near Cuernavaca, Aug. 2, 1896, *Pringle 7242* (US); bluffs of barranca near Cuernavaca, alt. 5000 ft., Aug. 10, 1898, *Pringle 6966* (MBG, NY, US).

### 3. *Thenardia gonoloboides* Woodson, spec. nov.

Suffrutices volubiles; ramulis teretibus tenuibus glabris; foliis oppositis breviter petiolatis lanceolatis apice anguste acuminatis basi obtusis tenuiter membranaceis glabris vel nervo medio subtus basi minutissime puberulis 4–8 cm. longis 1.3–2.5 cm. latis petiolo 0.5–1.0 cm. longo glabro; inflorescentiis foliis multo brevioribus multifloris; pedunculis primariis 0.5–1.2 cm. longis minute puberulo-papillatis secundariis vix manifestis; pedicellis 0.7–0.8 cm. longis minute puberulo-papillatis; bracteis anguste lanceolatis 0.1–0.3 cm. longis; calycis laciniis lineari-lanceolatis anguste acuminatis 0.5–0.7 cm. longis squamellis anguste oblongo-trigonalibus integris; corollae rotatae extus glabrae vel indistinctissime papillatae tubo 0.3–0.35 cm. longo basi ca. 0.125 cm. diametro metiente ostio ca. 0.25 cm. diametro metiente paulo supra medium abrupte constricto ubique staminifero lobis oblique obovatis obtusis 0.6–0.65 cm. longis patulis; staminum antheris valde exsertis 0.3–0.35 cm. longis filamentis 0.4 cm. longis indistinctissime papillatis; ovario ovoideo ca. 0.1 cm. longo glabro; nectariis haud crescentibus ovario ca. dimidio brevioribus; stigmate 0.1 cm. longo; folliculis ignotis.

Stems relatively slender, glabrous; leaves opposite, shortly petiolate, lanceolate, apex narrowly acuminate, base obtuse, 4–8 cm. long, 1.3–2.5 cm. broad, delicately membranaceous, glabrous, or very minutely puberulent at the base of the midrib beneath; petioles 0.5–1.0 cm. long, glabrous; inflorescence much shorter than the subtending leaves, multiflorous; primary

peduncle 0.5–1.2 cm. long, minutely puberulent-papillate, the secondary scarcely manifest; pedicels 0.7–0.8 cm. long, minutely puberulent-papillate; bracts narrowly lanceolate, 0.1–0.3 cm. long; calyx-lobes linear-lanceolate, narrowly acuminate, 0.5–0.7 cm. long, the squamellae narrowly oblong-trigonal, entire; corolla rotate, glabrous or very indistinctly papillate without, the tube 0.3–0.35 cm. long, base about 0.125 cm. in diameter, orifice about 0.25 cm. in diameter, abruptly constricted slightly above midway at the insertion of the stamens, the lobes obliquely obovate, obtuse, 0.6–0.65 cm. long, spreading; stamens conspicuously exserted, the anthers 0.3–0.35 cm. long, the filaments 0.4 cm. long, indistinctly papillate; ovary ovoid, 0.1 cm. long, glabrous; nectaries essentially separate, about half equalling the ovary; stigma 0.1 cm. long; follicles unknown.

MEXICO: OAXACA: canyons of mountains near Oaxaca, alt. 6500 ft., Aug. 20, 1894, *Pringle 4823* (MBG, TYPE, NY, US).

Closely related to the following species, from which it may be distinguished, in addition to the key characters, by the somewhat larger corolla in general, with tube constricted slightly above the middle, and by the larger anthers with filaments very indistinctly papillate.

4. *Thenardia Galeottiana* Baill. Bull. Soc. Linn. Paris 2: 819. 1890.

Stems relatively slender, glabrous; leaves opposite, petiolate, elliptic-lanceolate, apex acuminate, base obtuse, 3–9 cm. long, 0.6–2.5 cm. broad, membranaceous, glabrous above, beneath minutely puberulent in the lower axils of the midrib to glabrate; petioles 0.4–0.9 cm. long, glabrous; inflorescence much shorter than the subtending leaves, multiflorous; primary peduncle 0.4–0.6 cm. long, minutely puberulent-papillate, the secondary scarcely manifest; bracts lanceolate, 0.05–0.2 cm. long; calyx-lobes 0.4–0.6 cm. long, narrowly acuminate, minutely puberulent-papillate below, the squamellae oblong-dentiform, minutely erose; corolla rotate, glabrous or very indistinctly papillate without, the tube 0.2–0.25 cm. long, base

about 0.1 cm. in diameter, orifice about 0.2 cm. in diameter, abruptly constricted slightly below midway and there stamiferous, the lobes obliquely ovate, acute, 0.5–0.55 cm. long, spreading; stamens widely exerted, the anthers 0.25 cm. long, the filaments 0.2–0.25 cm. long, puberulent-papillate; ovary ovoid, about 0.07 cm. long, glabrous; nectaries equalling or slightly surpassing the ovary, essentially separate; stigma 0.1 cm. long; follicles unknown.

MEXICO: OAXACA: Talea, alt. 3000 ft., Aug., 1844, *Galeotti 1565* (MBG, NY, US, ISOTYPES); GUERRERO: Iguala Canyon, alt. 2500 ft., Sept. 21, 1905, *Pringle 13585* (G, US).

Galeotti reported the flowers of his specimens as “albidis,” which would appear to apply to the preceding species as well. However, unlike those of *Th. gonoloboides*, the tips of the corolla-lobes of *Th. Galeottiana* appear to be lined with pink upon the basis of herbarium specimens.

#### EXCLUDED SPECIES

*Thenardia* (?) *corymbosa* Benth. in Hook. Jour. Bot. 3: 246. 1841 = *Forsteronia umbellata* (Aubl.) Woodson, Ann. Mo. Bot. Gard. 22: 208. 1935 (*Apocynum umbellatum* Aubl. Hist. Pl. Gui. Fr. 1: 275; 3: pl. 108. 1775).

*Thenardia* (?) *laurifolia* Benth. Hook. Jour. Bot. 3: 246. 1841 = *Forsteronia laurifolia* (Benth.) A. DC. in DC. Prodr. 8: 438. 1844.

*Thenardia umbellata* (Aubl.) Spreng. Syst. 1: 636. 1825 (*Apocynum umbellatum* Aubl. Hist. Pl. Gui. Fr. 1: 275; 3: pl. 108. 1775) = *Forsteronia umbellata* (Aubl.) Woodson, Ann. Mo. Bot. Gard. 22: 208. 1935.

#### XXVI. PRESTONIA R. Br.

*Prestonia* R. Br. Mem. Wern. Soc. 1: 69. 1811; A. DC. in DC. Prodr. 8: 428. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 161. 1860; Benth. & Hook. Gen. Pl. 2: 709. 1876; Miers, Apoc. So. Am. 143. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895.

*Haemadictyon* Lindl. Trans. Hort. Soc. 6: 70. 1826; A. DC. loc. cit. 425. 1844; Muell.-Arg. loc. cit. 165. 1860; Miers, loc. cit. 254. 1878.

*Rhaptocarpus* Miers, loc. cit. 151. 1878.

*Temnadenia* Miers, loc. cit. 207. 1878, in part.

*Mitozus* Miers, loc. cit. 217. 1878, in part.

*Exothostemon* G. Don, according to Miers, loc. cit. 238. 1878, in part.

*Belandra* S. F. Blake, Contr. Gray Herb. 52: 78. 1917.

*Echites* of authors, in part, not P. Br.

Lactescent, suffruticose or suffrutescent lianas. Stems volubile, terete, the branches opposite, or opposite below becoming alternate above. Leaves opposite, entire, penninerved, eglandular; nodes stipulate. Inflorescence lateral, rarely subterminal, bostrychoidally racemose, frequently corymbose, bracteate. Calyx 5-parted, the lobes essentially equal, cleft nearly to the receptacle, imbricated, bearing within a solitary, opposite squamella. Corolla salverform, rarely infundibuliform, the tube straight or very rarely slightly gibbous, usually bearing 5 epistaminal appendages within, or exappendiculate, or the appendages replaced by vertical, callous ridges, the orifice bearing a callous, faucal annulus, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel sporangia borne ventrally near the apex of an enlarged, narrowly sagittate, peltate connective; pollen granular; filament short, subcylindrical, variously pubescent. Carpels 2, united at the apex by a common styler shaft surmounted by the fusiform or subcapitate, occasionally maniculate or digitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or completely conrescent. Follicles 2, apocarpous or more or less agglutinated, dehiscing along the ventral suture, containing many dry, truncate or inconspicuously rostrate, apically comose seeds.

Type species: *Prestonia tomentosa* R. Br. Mem. Wern. Soc. 1: 70. 1811.

## KEY TO THE SECTIONS

- A. Corolla exappendiculate within, the faucal annulus relatively tenuous and inconspicuous, not greatly thickened or tuberculate; anthers wholly included.....Sect. 1. COALITAE
- AA. Corolla appendiculate within (except in certain species of § *Tomentosae*), the faucal annulus conspicuously thickened or tuberculate; anther-tips exerted, often barely so (included in certain species of § *Tomentosae*).
  - B. Calyx-lobes relatively small and inconspicuous, only slightly foliaceous, usually more or less reflexed.....Sect. 2. ACUTIFOLIAE
- BB. Calyx-lobes relatively large and conspicuous, strikingly foliaceous or coriaceous, not reflexed.
  - C. Corolla glabrous or merely papillate without.....Sect. 3. ANNULARES
  - CC. Corolla densely pubescent without, at least the lobes...Sect. 4. TOMENTOSAE

Sect. 1. COALITAE Woodson. Relatively slender, glabrous (pubescent in *P. solanifolia*) lianas; leaves membranaceous; inflorescence simple, typically bostrychoid-racemose; calyx-lobes relatively inconspicuous, slightly foliaceous; corolla glabrous without, exappendiculate within, the faucal annulus relatively tenuous and inconspicuous, not greatly thickened and tuberculate; anthers wholly included. *Spp. 1-4.*

## KEY TO THE SPECIES

- a. Inflorescence relatively elongate, longer than the subtending leaves; corolla-lobes narrowly oblong-lanceolate; plants of the Antilles....1. *P. agglutinata*
- aa. Inflorescence corymbose, shorter than the subtending leaves; corolla-lobes obovate; species of South America.
  - b. Plants glabrous, or only the lower surface of the leaves inconspicuously puberulent-papillate.
    - c. Calyx-lobes lanceolate to oblong-lanceolate, acuminate; corolla-tube not inflated at the base.....2. *P. coalita*
  - cc. Calyx-lobes broadly obovate, rounded or obtuse; corolla-tube conspicuously inflated at the base.....3. *P. Dusenii*
- bb. Plants softly and densely ferruginous-puberulent, particularly the foliage.....4. *P. solanifolia*

1. *Prestonia agglutinata* (Jacq.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.

*Echites agglutinata* Jacq. Enum. Pl. Carib. 13. 1760.

*Echites adglutinata* Jacq. Stirp. Amer. 31. pl. 23. 1763;

A. DC. in DC. Prodr. 8: 448. 1844, not Burm., sphalm.

*Echites circinalis* Sw. Prodr. 52. 1788; A. DC. loc. cit. 466. 1844.

*Echites sanguinolenta* Tussac, Fl. Ant. 95. pl. 11. 1808.

*Haemadictyon circinalis* (Sw.) G. Don, Gen. Hist. 4: 83. 1838.

*Echites leptoloba* Stadelm. Flora 24<sup>1</sup>: Beibl. 15. 1841.

*Haemadictyon nutans* (Anders.) A. DC.  $\beta$  *sanguinolenta* (Tussac) A. DC. loc. cit. 426. 1844.

*Echites revoluta* A. DC. loc. cit. 457. 1844.

*Echites circinalis* Sw.  $\beta$  *Thomasiana* A. DC. loc. cit. 466. 1844.

*Temnadenia leptoloba* (Stadelm.) Miers, Apoc. So. Am. 211. 1878.

*Anechites adglutinata* (Jacq.) Miers, loc. cit. 236. 1878.

*Anechites circinalis* (Sw.) Miers, loc. cit. 1878.

*Anechites Thomasiana* (A. DC.) Miers, loc. cit. 237. 1878.

Plants completely glabrous; stems terete, relatively slender; leaves elliptic-oblong to broadly oval, apex shortly acuminate, base obtuse or rounded, 4–12 cm. long, 2–8 cm. broad, firmly membranaceous, opaque; petioles 1.2–2.5 cm. long; stipular appendages numerous, interpetiolar, minutely dentiform-flagelliform; racemes relatively elongate and lax, bearing 10–20 pale, greenish-white flowers; peduncle more or less flexuous, usually somewhat longer than the subtending leaves; pedicels 0.1–0.2 cm. long, somewhat accrescent after maturity; bracts ovate-lanceolate, scarious or somewhat subfoliaceous, about equalling the pedicels; calyx-lobes ovate-lanceolate, acuminate, essentially equal, 0.2–0.3 cm. long, scarious or slightly subfoliaceous, the internal squamellae deeply lacinate; corolla salverform, glabrous without, the tube 0.7–0.8 cm. long, about 0.1 cm. in diameter at the base, exappendiculate within, the fauceal annulus tenuous, relatively inconspicuous, the lobes obliquely oblong-lanceolate, acuminate, about 0.5 cm. long, reflexed; stamens inserted about midway within the corolla-tube, the anthers wholly included, narrowly lanceolate-sagittate, 0.5 cm. long, glabrous; ovary oblongoid, about 0.2 cm. long, abruptly produced into the style, glabrous; stigma 0.15 cm. long; nectaries narrowly compressed-oblongoid, separate, about half as long as the ovary; follicles unknown.



HISPANIOLA: HAITI: eastern La Hotte, Chapelle Mont Carmel, on the descent to Rio Bras Gauche, Nov. 8, 1924, *Ekman 2431* (S); Isle La Tortue, Basso-Terre, in coastal thickets, Oct. 28, 1925, *Ekman 5131* (S); Dept. du Nord, Bayeux, on the road to Aux Borgnes, Nov. 25, 1924, *Ekman 2664* (S); data incomplete, *Swartr s.n.* (S, MBG, photograph).

PORTO RICO: prope Cayey ad Pedro Avila, inter arbores *Coffeae Arabicae*, Sept. 22, 1895, *Sintenis 2457* (S).

It is possible that the specimen from Porto Rico may represent a chance introduction.

**2. *Prestonia coalita* (Vell.) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.**

? *Echites sulphurea* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 26. 1827; A. DC. in DC. Prodr. 8: 468. 1844.

*Echites coalita* Vell. Fl. Flum. 112. 1830; Icon. 3: pl. 40. 1827; A. DC. loc. cit. 458. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 155. 1860.

*Echites Vauthieri* A. DC. loc. cit. 457. 1844; Miers, Apoc. So. Am. 201. 1878.

*Echites Blanchetii* A. DC. loc. cit. 448. 1844; Muell.-Arg. loc. cit. 157. 1860.

*Echites Martii* Muell.-Arg. loc. cit. 155. 1860.

*Rhaptocarpus coalitus* (Vell.) Miers, loc. cit. 152. 1878.

*Rhaptocarpus apiculatus* Miers, loc. cit. 153. 1878.

*Rhaptocarpus Martii* (Muell.-Arg.) Miers, loc. cit. 1878.

*Mitozus Blanchetii* (A. DC.) Miers, loc. cit. 219. 1878.

*Mitozus concinnus* Miers, loc. cit. 223. 1878.

Stems terete, relatively slender, minutely and sparsely puberulent-papillate when young, soon becoming glabrate and conspicuously lenticellate; leaves oblong-lanceolate to rather broadly elliptic, apex acuminate, base obtuse to rounded, 5–15 cm. long, 2–6 cm. broad, firmly membranaceous, above glabrous, beneath puberulent-papillate to glabrate; petioles 0.5–1.0 cm. long; stipular appendages intrapetiolar, 2–4, minutely denticulate-flagelliform; racemes simple, more or less corymbose, bearing 8–20 pale greenish-yellow flowers; peduncle  $\frac{1}{2}$ – $\frac{1}{3}$  as long as the subtending leaves; pedicels 0.5–0.7 cm. long, somewhat accrescent after maturity, minutely puberulent-papillate

to glabrate; bracts ovate-lanceolate, 0.2–0.3 cm. long, subfoliaceous; calyx-lobes lanceolate to oblong-lanceolate, acuminate, 0.3–0.5 cm. long, foliaceous or subfoliaceous, minutely papillate to glabrate without, the internal squamellae deltoid, entire or somewhat erose; corolla salverform, glabrous or indistinctly papillate without, the tube 1.0–1.7 cm. long, about 0.15 cm. in diameter at the base, exappendiculate within, the faucal annulus tenuous, relatively inconspicuous, the lobes obliquely obovate, obtuse to shortly acuminate, 0.5–0.8 cm. long, reflexed; stamens inserted about midway within the corolla-tube, the anthers wholly included, narrowly lanceolate-sagittate, 0.5–0.6 cm. long, glabrous; ovary ovoid, abruptly produced into the style, about 0.1 cm. long, glabrous; stigma 0.15 cm. long; nectaries ovoid, separate, somewhat shorter than the ovary; follicles relatively slender, conspicuously moniliform, usually united at the tips, 20–45 cm. long, glabrous; seeds about 1 cm. long, the pale yellowish coma about 2.5 cm. long.

BRAZIL: CEARA: Crato, in "caapuerão," March 20, 1910, *Lofgren 620* (S); data incomplete, *Gardner 1755* (V); BAHIA: Jacobina, date lacking, *Blanchet 3613* (V); MINAS GERAES: Ilheus, 1859–60, *Wawra & Maly 279* (V); Praesidide de St. J. Bapt., date lacking, *Sellow 35* (V); Caldas Caxoeira, Jan. 26, 1826, *Widgren s.n.* (S); Caldas, 1857, *Regnell II 358* (S); Lagoa Santa, date lacking, *Warming s.n.* (C, S); RIO DE JANEIRO: Mandioca, date lacking, *Mikan s.n.* (V); Cantagallo, date lacking, *Pohl 5397* (V); Burity Pequeno, date lacking, *Pohl 2452* (V); data incomplete: *Widgren s.n.* (S); *Pohl 5168* (V); SÃO PAULO: prope Penha in districtu urbis S. Paulo, alt. 750 m., 1902, *Wacket s.n.* (V); Mooca, buschwald, Febr. 23, 1913, *Brade 5696* (S); Serra de Caracol, Dec. 25, 1875, *Mosen 4269* (S); PARANA: in silvula ad flumen Rio Tibagy pr. Ponta Grossa, Jan. 7, 1904, *Dusen s.n.* (S); same locality, March 17, 1909, *Dusen 3038* (S); Jaguarihyva, ad marginem silvae primacvae, alt. 740 m., May 8, 1914, *Jonsson 386a* (S, MBG); Capão Grande, in silvula, Dec. 23, 1903, *Dusen 2939* (S); RIO GRANDE DO SUL: Santo Angelo pr. Cachoeira, Jan. 16, 1893, *Malme 502* (S); Porto Alegre, Morro da Polieria, Cascatas, Dec. 16, 1901, *Malme 827* (S); Santo Angelo, Jan. 14, 1893, *Lindmann 957* (S); MATTO GROSSO: Santa Anna da Chapava, March 12, 1894, *Malme 1472* (S); Santa Cruz da Barra, in ripa dumetosa fluvii Paraguay, March 25, 1894, *Lindmann 3163* (S); DATA INCOMPLETE: *Widgren 1325* (S); *Biedel s.n.* (S).

**3. *Prestonia Dusenii* (Malme) Woodson, Ann. Mo. Bot. Gard. 18: 552. 1931.**

*Echites Dusenii* Malme, Arkiv f. Bot. **22A**<sup>2</sup>: 9. 1928.

Stems terete, relatively slender, minutely papillate when  
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young, glabrate and conspicuously lenticellate when fully mature; leaves broadly elliptic-oblong, apex subcaudate-acuminate, base obtuse or rounded, 5–15 cm. long, 2.5–6.0 cm. broad, above minutely and sparsely papillate to glabrate, minutely puberulent along the midrib, beneath minutely puberulent-papillate, firmly membranaceous; petioles 1.0–1.3 cm. long; stipular appendages interpetiolar, numerous, minutely denticiform; racemes corymbose, simple, bearing 5–12 greenish-yellow flowers; peduncle about as long as the subtending petioles; pedicels 0.7–0.8 cm. long, somewhat accrescent after maturity, minutely puberulent-papillate; bracts ovate, 0.1–0.3 cm. long, foliaceous; calyx-lobes obovate, minutely mucronulate, somewhat unequal, 0.5–0.7 cm. long, foliaceous, minutely papillate without at the base, the internal squamellae deltoid-trigonal, minutely lacerate; corolla salverform, minutely papillate without, the tube 1.0–1.3 cm. long, about 0.25 cm. in diameter at the base, conspicuously narrowing toward the orifice, exappendiculate within, the fauceal annulus tenuous, relatively inconspicuous, the lobes obovate, shortly acuminate, 0.7–0.8 cm. long, reflexed; stamens inserted somewhat below midway within the corolla-tube, the anthers wholly included, narrowly sagittate, about 0.5 cm. long, glabrous; ovary ovoid, 0.1 cm. long, glabrous; stigma 0.1 cm. long; nectaries compressed-ovoid, somewhat conerescent at the base, about half as long as the ovary; follicles relatively stout and rigid, united at the apex, 18–23 cm. long, glabrous; seeds not seen.

BRAZIL: PARANA: Alexandra, Serra da Prata, ad marg. silvae prim., March 5, 1911, *Dusen* 11486 (S, TYPE, MBG, photograph and analytical drawings); SÃO PAULO: Santos, Jan. 20, 1875, *Mosen* 3433 (S).

From slight intergradations observed, it is suspected that *P. Dusenii* and *P. coalita* may hybridize in the field.

4. *Prestonia solanifolia* (Muell.-Arg.) Woodson, comb. nov.  
*Haemadictyon* (?) *solanifolium* Muell.-Arg. in Mart. Fl.  
Bras. 6<sup>1</sup>: 171. pl. 49. 1860.

*Temnadenia solanifolia* (Muell.-Arg.) Miers, Apoc. So.  
Am. 214. 1878.

*Temnadenia corrugulata* Miers, loc. cit. 215. 1878.

*Temnadenia tenuicula* Miers, loc. cit. 216. 1878.

Stems terete, relatively stout, densely ferruginous-hirtellous, conspicuously lenticellate when fully mature; leaves elliptic to oval, apex acuminate, base obtuse or rounded, 7–13 cm. long, 3.5–7.0 cm. broad, firmly membranaceous, above minutely and relatively sparsely hirtellous-strigillose to glabrate, beneath densely ferruginous-hirtellous; petioles 0.9–1.3 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; racemes densely corymbose, bearing 15–40 bright yellow flowers; peduncle somewhat longer than the subtending petioles, minutely ferruginous-hirtellous; pedicels 0.7–1.0 cm. long, somewhat accrescent after maturity, minutely ferruginous-hirtellous; bracts lanceolate, 0.2–0.3 cm. long, subfoliaceous; calyx-lobes oblong-lanceolate, acuminate, 0.3–0.35 cm. long, subfoliaceous, rather sparsely and laxly ferruginous-pilosulose without, the internal squamellae deeply lacerate; corolla salverform, minutely papillate to glabrate without, the tube 0.8–1.0 cm. long, about 0.2 cm. in diameter at the base, ex-appendiculate within, the faucal annulus tenuous and relatively inconspicuous, the lobes obliquely obovate, shortly acuminate, 0.6–0.7 cm. long, widely spreading; stamens inserted somewhat below midway within the corolla-tube, the anthers wholly included, oblong-sagittate, 0.3–0.35 cm. long, glabrous; ovary broadly ovoid, about 0.1 cm. long, glabrous or very minutely papillate; stigma fusiform-subcapitate, 0.05 cm. long; nectaries compressed-ovoid, separate, nearly equalling the ovary; immature follicles relatively slender, continuous, united at the apex, densely ferruginous-hirtellous; seeds unknown.

BRAZIL: RIO DE JANEIRO (†): data incomplete, *Schüch s.n.* (V, TYPE, MBG, photograph and analytical drawings); MINAS GERAES: original forest, Matto Virgem, alt. 730 m., Nov. 21, 1930, *Mexia 5337* (MBG); data incomplete, 1831, *Ackermann s.n.* (M, COTYPE, MBG, photograph and analytical drawings); SÃO PAULO: Campinas, Nov., 1894, *Novaes 11302* (B).

The collection from São Paulo appears to differ from the more northerly specimen in having somewhat smaller flowers, but is too fragmentary to warrant segregation.

Sect. 2. *ACUTIFOLIAE* Woodson. Relatively slender, glabrous lianas; leaves membranaceous (coriaceous in *P. marginata*, *pachyphylla*, and *simulans*), usually veined with red or purple when young; inflorescence simple, typically bostrychoid-racemose; calyx-lobes relatively small and inconspicuous, only slightly foliaceous, usually more or less reflexed; corolla glabrous without, appendiculate within, the fauceal annulus conspicuously thickened; anther-tips exserted (except in *P. cyaniphylla* and *P. Hassleri*). *Spp.* 5-13.

#### KEY TO THE SPECIES

- a. Anthers rather deeply included; calyx-lobes broadly oblong, not sharply reflexed.
  - b. Leaves oblong-elliptic; corolla-tube not inflated at the base; plants of northern Bolivia.....5. *P. cyaniphylla*
  - bb. Leaves rhomboid-ovate to suborbicular; corolla-tube inflated at the base; species of Paraguay.....6. *P. Hassleri*
- aa. Anther-tips barely exserted, or at least attaining the orifice of the corolla-tube; calyx-lobes lanceolate, the tips reflexed.
  - b. Epistaminal appendages wholly included.
    - c. Leaves membranaceous; anthers pubescent dorsally, or very rarely glabrate.
      - d. Nectaries shorter than the ovary; follicles relatively stout, continuous; plants of Martinique, Guadeloupe, and Trinidad (including Tobago).....7. *P. quinquangularis*
      - dd. Nectaries as long as the ovary or somewhat longer; follicles relatively slender, slightly articulated; plants of Panama and South America.....8. *P. acutifolia*
    - cc. Leaves coriaceous; anthers glabrous.
      - d. Leaves acuminate, not heavily coriaceous, the venation verrucose above in desiccation.....9. *P. marginata*
      - dd. Leaves obtuse or rounded, frequently abruptly mucronulate, heavily coriaceous, the venation not verrucose above.....10. *P. pachyphylla*
  - bb. Epistaminal appendages slightly exserted, or at least attaining the orifice of the corolla-tube.
    - c. Leaves coriaceous or subcoriaceous.....11. *P. simulans*
    - cc. Leaves rather delicately membranaceous.
      - d. Leaves broadly rhombic-ovate to suborbicular; epistaminal appendages slightly exserted.....12. *P. Lindmanii*
      - dd. Leaves rather narrowly oblong-elliptic; epistaminal appendages attaining the orifice of the corolla-tube.....13. *P. lagoensis*

#### 5. *Prestonia cyaniphylla* (Rusby) Woodson, comb. nov.

*Echites cyaniphylla* Rusby, Bull. N. Y. Bot. Gard. 4: 409. 1907.

Stems relatively slender, minutely papillate when very young, soon becoming glabrate and conspicuously lenticellate when fully mature; leaves oblong-elliptic, apex acuminate, base obtuse to rounded, 6–8 cm. long, 2.5–4.0 cm. broad, membranaceous, above glabrous, or sparsely papillate at the base, opaque, beneath glabrous, subglaucous; petioles 1–2 cm. long; stipular appendages intrapetiolar, numerous, narrowly and minutely dentiform; racemes subcorymbose, simple, bearing 12–20 greenish-yellow flowers toward the end of the peduncle; peduncle usually somewhat longer than the subtending leaves, glabrous; pedicels 0.8–1.0 cm. long, somewhat accrescent after maturity, minutely papillate to glabrate; bracts narrowly oblong-lanceolate, 0.1–0.25 cm. long, subfoliaceous; calyx-lobes broadly oblong, acute to abruptly acuminate, 0.45–0.55 cm. long, foliaceous, ascending or slightly spreading, not sharply reflexed, glabrous without, the internal squamellae deltoid, slightly lacerate; corolla salverform, minutely papillate without, the proper-tube 1.2–1.5 cm. long, about 0.3 cm. in diameter at the base, slightly narrowing toward the middle, then again gradually expanding toward the orifice, epistaminal appendages very minute, wholly included, the faucal annulus conspicuously thickened, the lobes obliquely obovate, inconspicuously acuminate, 0.6–0.8 cm. long, reflexed or widely spreading; stamens inserted somewhat below midway within the corolla-tube, the anthers narrowly sagittate, about 0.5 cm. long, glabrous, rather deeply included; ovary ovoid-oblongoid, about 0.2 cm. long, glabrous; stigma 0.125 cm. long; nectaries compressed-ovoid, separate or somewhat concrescent at the base, somewhat shorter than the ovary; follicles relatively long and slender, continuous, agglutinated and united at the tip, 30–45 cm. long, glabrous; seeds about 0.4 cm. long, the pale tawny coma about 2 cm. long.

BOLIVIA: LA PAZ: Milluhuaya in Nord-Yungas, alt. 1200 m., Dec., 1917, *Buchtien 4372* (G, B); exact locality and date lacking, *Bang 2267* (MBG, NY, TYPE).

## 6. *Prestonia Hassleri* Woodson, spec. nov.

Suffruticosa volubilis omnino glabra; ramulis teretibus gracilibus maturitate conspicue lenticellatis; foliis rhomboi-

deo-ovatis vel suborbicularibus 4–10 cm. longis 3–7 cm. latis membranaceis supra olivaceis opacis subtus subglaucescentibus; petiolis 0.8–2.0 cm. longis; appendiculis stipulaceis intrapetiolariis multis minute dentiformibus; inflorescentiis racemosis simplicibus plurifloris; pedunculis folia aequantibus vel paulo superantibus; pedicellis 0.7–1.0 cm. longis post maturitatem paulo accrescentibus; bracteis anguste ovatis 0.2–0.3 cm. longis subfoliaceis; calycis laciniis late oblongis acutis vel abrupte acuminatis 0.4–0.5 cm. longis foliaceis ascendentibus patulisve haud reflexis intus basi squamellam deltiformem subintegram gerentibus; corollae salverformis virido-flavae tubo proprio 1.0–1.5 cm. longo basi ca. 0.35 cm. diametro metiente prope apicem sensim angustato appendiculis epistaminalibus minutis profunde inclusis annulo faucale manifeste incrassato lobis oblique obovatis breviter acuminatis 0.5–0.8 cm. longis patentibus; antheris anguste sagittatis 0.5–0.6 cm. longis glabris apice paulo exsertis; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus 0.15 cm. longo; nectariis compresse ovoideis integris ovario paulo brevioribus; folliculis juventate gracillimis paulo articulatis glabris agglutinatis; seminibus ignotis.

Plants completely glabrous; stems terete, relatively slender, conspicuously lenticellate when fully mature; leaves rhomboid-ovate or suborbicular, apex abruptly and shortly acuminate, base obtuse or rounded, 4–10 cm. long, 3–7 cm. broad, membranaceous, above olivaceous, opaque, beneath subglaucescent; petioles 0.8–2.0 cm. long; stipular appendages intrapetiole, numerous, minutely dentiform; inflorescence racemose, simple, bearing 20–40 greenish-yellow flowers; peduncle about as long as the subtending leaves or somewhat longer; pedicels 0.7–1.0 cm. long, somewhat accrescent after maturity; bracts narrowly ovate, 0.2–0.3 cm. long, subfoliaceous; calyx-lobes broadly oblong, acute or abruptly acuminate, 0.4–0.5 cm. long, foliaceous, ascending or somewhat spreading, not reflexed, the internal squamellae deltoid, subentire; corolla salverform, glabrous without, the proper-tube 1.0–1.5 cm. long, about 0.35 cm. in diameter at the base, conspicuously narrowed toward the ori-

filice, epistaminal appendages minute, deeply included, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.5–0.8 cm. long, reflexed or widely spreading; stamens inserted somewhat below midway within the corolla-tube, the anthers narrowly sagittate, 0.5–0.6 cm. long, the tips slightly exerted or at least attaining the orifice of the corolla-tube, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries compressed-ovoid, separate, somewhat shorter than the ovary; immature follicles relatively long and slender, slightly articulated, agglutinated and united at the apex, glabrous; seeds unknown.

PARAGUAY: in regione lacus Ypacaray, March, 1913, *Hassler 12527* (B, C, MBG, TYPE); common in hedges, Villa-Rica, March 12, 1929, *Jørgensen 4182* (MBG); in regione collium, Cordillera de Villa-Rica, Jan., 1905, *Hassler 8765* (B); in sylva, San Bernardino, Dec., year lacking, *Hassler 3583* (B, BB, V); Cordillera de Altos, Oct., 1902, *Fuebrig 64a* (B, DL, G, M).

This species is very close to the preceding, of which it may eventually be proved a variety.

**7. *Prestonia quinquangularis* (Jacq.) Spreng. Syst. 1: 637. 1825.**

*Echites quinquangularis* Jacq. Enum. Pl. Carib. 13. 1760; Stirp. Amer. 32. pl. 25. 1763; A. DC. in DC. Prodr. 8: 468. 1844.

*Echites nutans* Anders. Trans. Soc. Arts Lond. 25: 203. 1807; Sims, Bot. Mag. 51: pl. 2473. 1824.

*Haemadictyon venosum* Lindl. Trans. Hort. Soc. 6: 70. 1826; Miers, Apoc. So. Am. 255. 1878.

*Haemadictyon nutans* (Anders.) A. DC. loc. cit. 426. 1844.

*Temnadenia quinquangularis* (Jacq.) Miers, loc. cit. 217. 1878.

Stems relatively slender, glabrous, inconspicuously lenticellate when fully mature; leaves oblong- to ovate-elliptic, acute to shortly acuminate, base obtuse to rounded, 6–14 cm. long, 2–6 cm. broad, membranaceous, conspicuously veined with red or purple when young, above glabrous, beneath minutely papillate to glabrous; petioles 1–2 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; inflores-



cence racemose, simple, bearing 6–20 greenish-yellow flowers; peduncle about as long as the subtending leaves or somewhat shorter, glabrous; pedicels 0.7–1.5 cm. long, somewhat accrescent after maturity, glabrous; bracts ovate-lanceolate, 0.1–0.15 cm. long, subfoliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.15–0.2 cm. long, subfoliaceous, sharply reflexed, glabrous without, the internal squamellae deltoid-ligulate, minutely erose; corolla salverform, minutely papillate without, 1.2–1.5 cm. long, about 0.3 cm. in diameter at the base, the epistaminal appendages about 0.1 cm. long, wholly included, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate to obtuse, 0.7–1.0 cm. long, sharply reflexed; stamens inserted slightly above midway within the corolla-tube, the anthers narrowly sagittate, 0.55–0.6 cm. long, pubescent dorsally; ovary ovoid, about 0.2 cm. long, glabrous; nectaries compressed-ovoid, separate or more or less conerescent at the base, somewhat shorter than the ovary; follicles relatively stout, continuous, agglutinated and united at the apex, 20–35 cm. long, glabrous; seeds about 1 cm. long, the tawny coma 2.0–2.5 cm. long.

MARTINIQUE: Pelée, date lacking, *Kunth s.n.* (B).

GUADELOUPE: prope Capesterre, 1892, *Duss 2841* (B); route de Pigeon à la Ponte Noire, Dec. 28, 1895, *Duss 3713* (B).

TRINIDAD: Caparo, April 27, 1908, *Broadway 2707* (B); St. Clair Experiment Station, wild on fences, May 22, 1907, *Broadway 2582* (B, M); O'Meara Savannah, Arima, April 16, 1908, *Broadway 2799* (B); Montpelier, Tobago, running over shrubs and grasses, Oct. 3, 1909, *Broadway 3132* (B); Tobago ad Wellbeck, Nov. 23, 1912, *Broadway 4350* (B); exact locality and date lacking, *von Rohr 23* (C).

The purple venation of the leaves is said by collectors to be replaced by white not infrequently. This species has also been reported locally from Venezuela and the Guianas.

**8. *Prestonia acutifolia* (Benth.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895.**

*Haemadictyon acutifolium* Benth. ex Muell.-Arg. in Mart.

Fl. Bras. 6<sup>1</sup>: 167. 1860; Miers, Apoc. So. Am. 260. 1878.

*Haemadictyon acutifolium* Benth.  $\beta$  *latifolium* Muell.-Arg. loc. cit. 1860.

*Haemadictyon calignosum* Miers, loc. cit. 1878.

*Echites Bangii* Rusby, Bull. N. Y. Bot. Gard. 4: 409. 1907.

*Echites Hulkiana* Pulle, Rec. Trav. Bot. Néerl. 9: 160. 1912.

*Echites Laurentiae-disca* Rusby, Descr. So. Am. Pl. 85. 1920.

*Prestonia acutifolia* (Benth.) K. Sch. var. *latissima* Mgf. Notizblatt 9: 982. 1926.

Stems relatively slender, minutely puberulent when young, glabrate and conspicuously lenticellate when fully mature; leaves elliptic to oblong- or ovate-elliptic, apex acuminate, base obtuse or rounded, firmly membranaceous, usually veined with red or purple when young, above dark green, opaque, glabrous, beneath somewhat paler, minutely and irregularly papillate to glabrous, 6–16 cm. long, 2–8 cm. broad; petioles 0.6–2.0 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence racemose, simple, bearing 6–40 greenish-yellow flowers; peduncle usually somewhat shorter than the subtending leaves, occasionally somewhat longer, glabrous; pedicels 0.5–1.2 cm. long, somewhat accrescent after maturity, glabrous or very minutely papillate; bracts ovate-lanceolate, 0.1–0.2 cm. long, subfoliaceous; calyx-lobes narrowly ovate-lanceolate, acuminate, 0.15–0.2 cm. long, sharply reflexed, subfoliaceous, minutely papillate to glabrous without, the internal squamellae deltoid-liguliform, minutely lacerate or erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.5–2.0 cm. long, about 0.4 cm. in diameter at the base, epistaminal appendages 0.05–0.2 cm. long, wholly included, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–1.0 cm. long, sharply reflexed; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers rather broadly sagittate, 0.4–0.55 cm. long, pubescent dorsally, rarely glabrate; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.1 cm. long; nectaries compressed-oblongoid, separate or more or less concrescent, somewhat surpassing, or about equalling the ovary; follicles relatively long and slender, obscurely and rather distantly articulated, ag-

glutinated and united at the apex, usually rather tortuous, 20–40 cm. long, glabrous, or very indistinctly papillate; seeds 0.1 cm. long, the coma pale tawny, 3–4 cm. long.

PANAMA: CANAL ZONE: shore s. of Barbour Trail, Barro Colorado Island, Febr. 12, 1932, *Woodworth & Vestal 498* (FM).

COLOMBIA: SANTANDER: alluvial flat, alt. 80–90 m., Badillo, Jan. 16, 1918, *Pennell 3912* (NY); Rio Surata Valley, between Bucaramanga and El Jaboneillo, alt. 800–1500 m., Jan. 2, 1927, *Killip & Smith 16305* (NY, US); upper Rio Lehrija Valley, northwest of Bucaramanga, alt. 400–700 m., Dec. 29, 1926, *Killip & Smith 16308* (US, NY, B); MAGDALENA: open grass and thickets, rare, near Bonda, alt. 250 m., Nov. 9, Cienaga, Sept. 10, 1898, *H. H. Smith 1645* (NY); ANTIOQUIA: Pto. Berrio, near Medellin, June 20, 1928, *Toro 1105* (NY).

VENEZUELA: DISTRITO FEDERAL: Caracas, date lacking, *collector unknown* (S); DATA INCOMPLETE: May, 1896, *Eusby & Squires 302* (B, M, MBG, NY); AMAZONAS: ad fl. Casiquiari, 1853–54, *Spruce 3430* (V).

DUTCH GUIANA: on river banks, fluv. Lucie, Nov. 26, 1910, *Hulk 303* (U).

BRAZIL: AMAZONAS: in vicinibus Barra, Prov. Rio Negro, Dec., 1850–March, 1851, *Spruce 1002* (B, Camb., M, TYPE, V); Bôa Vista, Rio Branco super., in silvis ripariis, July, 1913, *Kuhlmann 3650* (B); MATTO GROSSO: Cuyaba, July 2, 1903, *Malme 3122* (S); in “cerrado” pr. oppidium Cuyaba, March 22, 1904, *Malme 1478* (B, DL, S); ad villam Cuyabensis, date lacking, *Manso & Lhotsky 37* (B); DATA INCOMPLETE: *Martius s.n.* (M); *Glazou 20412* (B).

PERU: LOBETO: Puerto Arturo, lower Rio Huallaga below Yurimaguas, dense forest, alt. about 135 m., Aug. 24–25, 1929, *Killip & Smith 27840* (MBG, US); Amaqueria, Stromgebiet des Ucayali von 10° S. bis zur Mündung, Nov. 24, 1923, *Tessmann 3368* (B, DL); Mündung des Apaga, Stromgebiet des Marañon von Jquitos aufwärts bis zur Santiago-Mündung am Pongo de Manseriche, ca 77° 30' West., alt. 145 m., Dec. 23, 1924, *Tessmann 4816* (B); Mishuyacu, near Iquitos, alt. 100 m., forest, April, 1930, *Klug 1119* (NY, US); HUANUCO: zwischen Monzon und den Huallaga, alt. 600–700 m., Aug. 28, 1903, *Weberbauer 3605* (B, DL); JUNIN: thickets, La Moiced, alt. about 700 m., May 29–June 4, 1929, *Killip & Smith 33387* (MBG, US); in sunny montana along stream, same locality, Aug. 10–24, 1923, *Macbride 5345* (B, FM); SAN MARTIN: Alto Rio Huallaga, alt. 360–900 m., Dec., 1929, *Williams 5550* (FM, MBG).

BOLIVIA: SANTA CRUZ: bosques de Buenavista, alt. 450 m., April 22, 1917, *Steinbach 3331* (B); quintas de la ciudad de Santa Cruz, alt. 450 m., Febr. 20, 1917, *Steinbach 3256* (B); BENI: Rurrenabaque, alt. 1000 ft., Dec. 1, 1921, *Cardenas 1748* (NY); DATA INCOMPLETE: *Bang 3053* (B, MBG, NY).

PARAGUAY: in reg. cursus superioris fl. Apa, Dec., 1901, *Hassler 8173* (B, BB, V); in reg. vicine San Estanislao, Jan., year lacking, *Hassler 6001* (B, BB); Centurion, Jan. 5, 1909, *Fiebrig 4541* (B); in altaplanitie et declivibus “Sicera de Amambay,” March, 1908, *Eojas 10370* (B).

ARGENTINA: FORMOSA: Villa, Febr., 1918, *Jørgensen 3119* (B, BA, MBG).

It is not improbable that an accumulation of additional specimens will necessitate the segregation of *P. acutifolia* as

interpreted in this revision. At the present moment the number of specimens appears too scanty, considering the vast geographical distribution of the species, to merit division into subsidiary units.

9. *Prestonia marginata* (Benth.) Woodson, comb. nov., not Mgf.

*Haemadictyon marginatum* Benth. in Hook. Jour. Bot. 3: 250. 1841; A. DC. in DC. Prodr. 8: 426. 1844; Miers, Apoc. So. Am. 256. 1878.

*Haemadictyon Cayennense* A. DC. loc. cit. 427. 1844; Miers, loc. cit. 1878.

*Haemadictyon papillosum* Muell.-Arg. Linnaea 30: 432. 1860.

Stems terete, relatively slender, minutely and sparsely hispidulous when young, glabrate, or scabridulous in the vicinity of the nodes, and rather inconspicuously lenticellate when fully mature; leaves oblong-elliptic, apex acuminate to subcaudate-acuminate, base acute to obtuse, 6–12 cm. long, 2–5 cm. broad, glabrous, coriaceous, but not very thickly so, either surface somewhat nitidulous, the venation more or less verrucose throughout; petioles 0.3–0.4 cm. long; stipular appendages interpetiolar, 6–8, minutely dentiform; inflorescence racemose, simple, or rarely dichotomous, bearing 10–40 pinkish-yellow flowers; peduncle about equalling or somewhat surpassing the subtending leaves; pedicels 0.8–1.5 cm. long, somewhat accrescent after maturity, glabrous or very minutely and sparsely papillate; bracts ovate-lanceolate, 0.8–1.0 cm. long, scarious; calyx-lobes ovate-lanceolate, acuminate, 0.2–0.3 cm. long, somewhat reflexed or spreading, glabrous to very irregularly papillate without, the internal squamellae deltoid, somewhat cleft or divided; corolla salverform, glabrous without, 1.3–1.7 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages 0.05–0.07 cm. long, wholly included, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the

anthers oblong-sagittate, 0.5 cm. long, glabrous; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.1 cm. long; nectaries compressed-ovoid, separate or somewhat conerescent at the base, somewhat shorter than the ovary; follicles relatively slender, continuous or very obscurely articulated, usually somewhat falcate and united at the apex, 11–16 cm. long, glabrous; seeds about 1.1 cm. long, shortly rostrate, the pale yellowish coma about 2.5 cm. long.

BRITISH GUIANA: Pirara, date uncertain, *Schomburgk 713* (K, TYPE); banks of the Potaro River, Tumatumari, July 4–6, 1921, *Gleason 336* (NY, US); Malali, Demerara River, lat. about 5° 35' N., Oct. 30–Nov. 5, 1922, *Cruz 2631* (G).

FRENCH GUIANA: Cayenne, date lacking, *Vargas s.n.* (DC).

BRAZIL: PARA: overflow bank, Rio Thome Assu, Distrito Acara, alt. 35 m., Aug. 1, 1931, *Mexia 6029* (MBG).

#### 10. *Prestonia pachyphylla* Woodson, nom. nov.

*Prestonia marginata* Mgf. Notizblatt 9: 88. 1924, not *Haemadictyon marginatum* Benth. (*Prestonia marginata* (Benth.) Woodson).

Stems relatively stout, minutely and rather sparsely pilosulose when very young, glabrate, or minutely scabridulous in the vicinity of the nodes, and rather inconspicuously lenticellate when fully mature; leaves broadly oval, apex obtuse to rounded, frequently abruptly mucronulate, base broadly obtuse to rounded, 6–12 cm. long, 2–4 cm. broad, glabrous, heavily coriaceous, either surface somewhat nitidulous, below somewhat glaucescent, the venation not verrucose above; petioles 0.5–0.8 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence racemose, simple, bearing 20–40 greenish-yellow flowers; peduncle glabrous to very inconspicuously papillate, somewhat surpassing the subtending leaves; pedicels 0.7–1.0 cm. long, somewhat accrescent after maturity, glabrous to very inconspicuously papillate; calyxlobes ovate-lanceolate, acuminate, 0.3–0.4 cm. long, somewhat reflexed or spreading, glabrous without, the internal squamellae somewhat incised or divided; corolla salverform, glabrous or very inconspicuously papillate without, 1.2–1.3 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages 0.2–0.25 cm. long, wholly included, the faucal an-

nulus conspicuously thickened, the lobes obliquely obovate, rounded, 0.8–1.0 cm. long, reflexed; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, about 0.5 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.1 cm. long; nectaries compressed-oblongoid, somewhat surpassing the ovary, separate or somewhat con-crescent at the base; follicles unknown.

BRAZIL: AMAZONAS: Serra de Mairary, Surumu, Rio Branco, Nov., 1909, *Ule* 8451 (B, TYPE, MBG, photograph and analytical drawings).

**11. *Prestonia simulans* Woodson, spec. nov.**

Suffruticosa vel fruticosa volubilis; ramulis gracilibus glabris maturitate rimulosis inconspicueque lenticellatis; foliis oblongo-ellipticis apice obtusis minute mucronatis basi obtusis 8–10 cm. longis 3–4 cm. latis coriaceis subcoriaceisve glaberrimis supra plus minusve illustribus subtus opacis margine post exsiccationem leviter revolutis; petiolis 0.2–0.3 cm. longis glabris; inflorescentiis lateralibus simplicibus foliis subaequantibus flores gilvos 8–10 laxe gerentibus; pedunculo glaberrimo parte tertia superiore florifero; pedicellis 1.3–1.5 cm. longis glabris; bracteis minute ovato-lanceolatis vix bene visis; calycis laciniis ovato-lanceolatis acuminatis apice plus minusve reflexis 0.4–0.45 cm. longis subfoliaceis glaberrimis intus basi squamellam deltoideo-ligulatam integram vel irregulariter bifidam gerentibus; corollae salverformis tubo 0.9–1.0 cm. longo basi ca. 0.125 cm. diametro metiente supra basi aliquid ampliato deinde ad insertionem staminum gradatim angustato faucibus ca. 0.15 cm. diametro metientibus extus glabris intus prope insertionem staminum minute retrorseque barbatis appendicibus epistaminalibus linearibus ca. 0.2 cm. longis paulo exsertis annulo faucium conspicue incrassato, lobis oblique obovato-dolabriformibus breviter acuminatis 1.0–1.2 cm. longis patentibus; antheris lanceolato-sagittatis 0.5 cm. longis glabris apice exsertis; ovario ovoideo ca. 0.2 cm. longo glabro; stigmatibus 0.1–0.125 cm. longo; nectariis compressis ovoideis haud con-crescentibus ca. 0.15 cm. longis; folliculis ignotis.

Stems relatively slender, glabrous, rimulous and inconspicuously lenticellate at maturity; leaves opposite, shortly petiolate, oblong-elliptic, apex obtuse, minutely mucronate, base obtuse, 8–10 cm. long, 3–4 cm. broad, coriaceous or subcoriaceous, above more or less lustrous, beneath opaque, the margin somewhat revolute in desiccation; petioles 0.2–0.3 cm. long, glabrous; inflorescence simple, relatively lax, about equalling the subtending leaves, bearing 8–10 yellowish flowers; peduncle glabrous, the upper third floriferous; pedicels 1.3–1.5 cm. long, glabrous; bracts minutely ovate-lanceolate, very minute; calyxlobes ovate-lanceolate, acuminate, the tips more or less reflexed, 0.4–0.45 cm. long, subfoliaceous, glabrous, the internal squamellae deltoid-ligular, entire or irregularly bifid; corolla salverform, the tube 0.9–1.0 cm. long, about 0.125 cm. in diameter at the base, somewhat inflated below midway, thence gradually constricted toward the insertion of the stamens, about 0.15 cm. in diameter at the orifice, glabrous without, retrorsely barbate above the insertion of the stamens within, epistaminal appendages linear, about 0.2 cm. long, somewhat exerted, faucal annulus conspicuous, the lobes obliquely obovate-dolabriform, shortly acuminate, 1.0–1.2 cm. long, reflexed; anthers lanceolate-sagittate, 0.5 cm. long, glabrous, the tips exerted; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.1–0.125 cm. long; nectaries compressed-ovoid, not conerescent, about 0.15 cm. long; follicles unknown.

COLOMBIA: CUNDINAMARCA: Tocaima, Dec., 1932, *Arbelaes* 2140 (US, TYPE, MBG, analytical drawings).

Closely approaching the habit of *P. pachyphylla*, from which it differs in the exertion of the epistaminal appendages.

**12. *Prestonia Lindmanii*** (Malme) Hoehne, Comm. Linh. Electr. Estrat. Matto Grosso, Anexo 5, Bot. 6: 88. 1915.

*Haemadictyon Lindmanii* Malme, Bihang till K. Sv. Vet. Akad. Handl. Afd. III. 24<sup>10</sup>: 31. pl. 3. fig. 10. 1899.

Stems relatively slender, minutely puberulent-papillate when very young, soon becoming glabrate and rather inconspicuously lenticellate; leaves broadly rhombic-ovate to sub-

orbicular, apex shortly and frequently very abruptly acuminate, base obtuse to rounded, 5–10 cm. long, 3–7 cm. broad, membranaceous, glabrous, or very minutely puberulent-papillate when very young, either surface opaque, the lower somewhat paler; petioles 1–3 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform-flagelliform; inflorescence racemose, simple, bearing 10–40 greenish-yellow flowers; peduncle glabrous, usually equalling or somewhat surpassing the subtending petioles; pedicels 1.0–1.25 cm. long, somewhat accrescent after maturity, glabrous; bracts ovate to ovate-lanceolate, 0.15–0.2 cm. long, subfoliaceous; calyx-lobes ovate-lanceolate, acute to acuminate, 0.25–0.35 cm. long, subfoliaceous, glabrous or very inconspicuously papillate without, the internal squamellae deltoid, somewhat incised or lacerate; corolla salverform, glabrous or very minutely papillate without, the tube 1.7–2.0 cm. long, about 0.4 cm. in diameter at the base, epistaminal appendages 0.35–0.45 cm. long, slightly exserted, the faucal annulus conspicuously thickened, the lobes obliquely obovate, inconspicuously acuminate, 0.8–1.0 cm. long, reflexed; stamens inserted at about the upper  $\frac{1}{4}$  of the corollatube, the anthers oblong-sagittate, 0.5 cm. long, glabrous, the tips slightly exserted; ovary ovoid, about 0.25 cm. long, glabrous; stigma 0.15–0.2 cm. long; nectaries compressed-ovoid, separate or somewhat concrescent at the base, about equalling the ovary; follicles relatively long and slender, continuous or essentially so, separate and parallel, or slightly agglutinated when immature, 30–35 cm. long, glabrous; seeds 0.8–1.0 cm. long, shortly rostrate, the pale tawny coma about 2.5 cm. long.

BRAZIL: RIO DE JANEIRO: exact locality and date lacking, *Glazion 12943, 14072* (B); MATTO GROSSO: Cuyaba, Febr., 1832, *Manso & Lhotsky 33* (B, DL); Corumba, April 7, 1903, *Malme s.n.* (S); in ripa dumetosa fluvii Paraguay, Santa Cruz da Barra, March 25, 1894, *Lindmann 43161* (S, TYPE, MBG, photograph and analytical drawings); Toscana, Caceres, Jan., 1909, *Hoehne 1200* (B).

PARAGUAY: in reg. cursus superioris fl. Apa, Dec., 1901, *Hassler 8065* (B, BB, V); exact locality and date lacking, *Hassler 3061* (BB).

The collections of Glazion represented as from Rio de Janeiro are open to suspicion. The inaccuracy of Glazion's labels is notorious.



**13. *Prestonia lagoensis* (Muell.-Arg.) Woodson, comb. nov.**

*Haemadictyon Lagoense* Muell.-Arg. in Warming, Viden-  
skab. Meddel. Nat. Foren. Kjoeb. 115. 1869.

*Haemadictyon Warmingii* Muell.-Arg. loc. cit. 116. 1869.

Plants completely glabrous; stems relatively slender, inconspicuously lenticellate when fully mature; leaves rather narrowly oblong-elliptic, apex acuminate, base acute, 6.5–10.5 cm. long, 2.3–4.2 cm. broad, membranaceous, either surface opaque, the lower somewhat paler; petioles 0.7–1.7 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence racemose, simple, bearing 10–30 greenish-yellow flowers; peduncle somewhat lax and flexuous, somewhat surpassing the subtending leaves; pedicels 1.5–1.8 cm. long; bracts lanceolate, 0.1–0.15 cm. long, subfoliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.3–0.36 cm. long, subfoliaceous, the internal squamellae deltoid-ligular, inconspicuously incised or divided; corolla salverform, glabrous without, the tube 1.3–1.5 cm. long, about 0.35 cm. in diameter at the base, the epistaminal appendages about 0.2 cm. long, attaining the orifice, the faucal annulus conspicuously thickened, the lobes obliquely obovate, acuminate, 0.7–0.8 cm. long, reflexed; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, 0.5 cm. long, glabrous, the tip barely exerted or at least attaining the orifice of the corolla-tube; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.125 cm. long; nectaries compressed-ovoid, about equalling or slightly surpassing the ovary, separate or somewhat conerescent at the base; follicles unknown.

BRAZIL: MINAS GERAES: Lagoa Santa, 1870, *Warming s.n.* (C, TYPE, S, MBG, photograph and analytical drawings).

It is quite possible that this is merely a variety of the preceding.

Sect. 3. ANNULARES Woodson. Relatively stout (except in *P. exserta*, *P. velutina*, and *P. parvifolia*), glabrous or softly pubescent lianas; leaves membranaceous to coriaceous; inflorescence simple or variously compound, typically bostrychoid-

racemose to subumbellate; calyx-lobes relatively large and conspicuous, foliaceous, petalaceous, or coriaceous; corolla glabrous or minutely papillate without, appendiculate within, the faucal annulus conspicuously thickened; anther-tips exerted, or at least attaining the faucal annulus. *Spp.* 14-45.

## KEY TO THE SPECIES

- A. Nectaries thick and fleshy (see also 37-38), separate, or only united at the base; species of South America (including Trinidad and Tobago), and Panama.
- B. Suffrutescent lianas; calyx-lobes foliaceous, uniformly green (see also 19, 34, 39).
- C. Anthers glabrous; leaves not cordate.
- D. Epistaminal appendages surpassing the anthers, inserted at the base of the faucal annulus, or slightly below.
- E. Bracts relatively inconspicuous, linear to linear-lanceolate, 0.1-0.5 cm. long, only slightly foliaceous.....14. *P. caserta*
- EE. Bracts very conspicuous, elliptic to obovate-lanceolate, 0.7-1.0 cm. long, manifestly foliaceous.....15. *P. velutina*
- DD. Epistaminal appendages much surpassed by the anthers, inserted well below the faucal annulus.
- E. Bracts conspicuously foliaceous, nearly as large as the calyx-lobes; leaves finely puberulent beneath; plants of Ecuador....
- .....16. *P. parvifolia*
- EE. Bracts relatively inconspicuous, only slightly foliaceous, much smaller than the calyx-lobes; leaves glabrous beneath, or essentially so; plants of (southern ?) Brazil.....17. *P. perplexa*
- CC. Anthers minutely pubescent dorsally; leaves usually obscurely and broadly cordate, at least in part, occasionally only somewhat truncate or rounded at the base.....18. *P. mollis*
- BB. Fruticose or suffruticose lianas; calyx-lobes petalaceous or coriaceous, usually more or less suffused or tinted with purple, at least the pedicels so colored.
- C. Epistaminal appendages deeply included.
- D. Inflorescence simple; anthers glabrous.....19. *P. didyma*
- DD. Inflorescence compound; anthers minutely pubescent dorsally.
- E. Calyx-lobes 0.7-1.0 cm. long.
- F. Corolla-lobes about half as long as the tube; leaves acute to obtuse.....20. *P. annularis*
- FF. Corolla-lobes about as long as the tube, or nearly so; leaves acuminate.....21. *P. guianensis*
- EE. Calyx-lobes 1.0-1.8 cm. long.
- F. Inflorescence dichotomous or rarely trichotomous; calyx greenish or somewhat suffused with purple.
- G. Calyx-lobes about as long as the corolla-tube, delicately membranaceous.

- H. Calyx-lobes 1.7-1.8 cm. long, somewhat suffused with purple; corolla "raisin purple," the tube 1.7-1.9 cm. long, the lobes 1.0-1.2 cm. long; anthers minutely papillate.....22. *P. purpurissata*
- HH. Calyx-lobes 1.2-1.3 cm. long, greenish; corolla yellowish-pink, the tube 1.2-1.3 cm. long, the lobes 1.4-1.5 cm. long; anthers pilosulose.....*P. discolor*  
(See Addenda)
- GG. Calyx-lobes manifestly shorter than the corolla-tube, coriaceous or subcoriaceous.
- H. Leaves delicately membranaceous; corolla-tube gradually constricting toward the orifice; plants of northeastern Brazil.....23. *P. finitima*
- HH. Leaves subcoriaceous; corolla-tube not constricting toward the orifice; plants of eastern Peru and Bolivia.....  
.....24. *P. Phenax*
- FF. Inflorescence branching repeatedly; calyx deep purple.....  
.....25 *P. Brittonii*
- CC. Epistaminal appendages exerted, or at least attaining the faucal annulus.
- D. Plants glabrous (very minutely puberulent-papillate generally in 34), or only the inflorescence minutely puberulent to glabrate.
- E. Inflorescence compound, or rarely simple; corolla-tube 1.2-2.3 cm. long.
- F. Inflorescence greatly surpassing the subtending leaves; calyx-lobes delicately membranaceous.....26. *P. laxa*
- FF. Inflorescence much shorter than the subtending leaves; calyx-lobes coriaceous or subcoriaceous.
- G. Calyx-lobes 0.9-1.6 cm. long; inflorescence di- or trichotomous.
- H. Bracts very conspicuous, more or less foliaceous or petalaceous, caducous (except in 29).
- I. Epistaminal appendages barely attaining the faucal annulus; flowers yellow; plants of Ecuador.....  
.....27. *P. rotundifolia*
- II. Epistaminal appendages exerted.
- J. Inflorescence corymbose, manifestly dichotomous; bracts caducous; flowers greenish-white or -yellow; plants of eastern Bolivia.....28. *P. robusta*
- JJ. Inflorescence densely subumbellate-capitate; bracts persistent; flowers reddish, tinted with purple, yellow, and white; plants of northern Brazil.....  
.....29. *P. macroneura*
- HH. Bracts very inconspicuous, scarious, persistent.
- I. Corolla-tube essentially glabrous without; anthers glabrous.....30. *P. trifida*
- II. Corolla-tube minutely velutinous without; anthers minutely puberulent dorsally.....31. *P. vana*

- GG. Calyx-lobes 0.5–0.8 cm. long; inflorescence dichotomous or simple.
- H. Leaves obovate to obovate-lanceolate, apex obtuse or rounded; inflorescence dichotomous; squamellae entire or only slightly erose.....32. *P. plumierifolia*
- HH. Leaves broadly oval, shortly acuminate; inflorescence simple or obscurely dichotomous; squamellae deeply lacerate.....33. *P. amazonica*
- EE. Inflorescence simple; corolla-tube 0.7–1.5 cm. long.
- F. Leaves completely glabrous; calyx-lobes 0.9–1.0 cm. long; plants of northern and central Brazil.....34. *P. Lindleyana*
- FF. Leaves puberulent when young, persistently papillate beneath; calyx-lobes 0.4–0.65 cm. long; plants of southeastern Brazil.....35. *P. denticulata*
- DD. Plants more or less densely ferruginous-pubescent throughout.....36. *P. Meg'agros*
- AA. Nectaries thin and more or less diaphanous (except in 37 38), concrecent (frequently irregularly lacerate); species of Central America (including Panama) and Ecuador.
- B. Nectaries more or less thick and fleshy throughout, completely concrecent.
- C. Inflorescence di- or trichotomous, much shorter than the subtending leaves; calyx-lobes 1.0–1.2 cm. long.....37. *P. obovata*
- CC. Inflorescence simple, about as long as the subtending leaves or nearly so; calyx-lobes 0.4–0.5 cm. long.....38. *P. concolor*
- BB. Nectaries thin and more or less diaphanous, at least the margins, concrecent (frequently irregularly lacerate).
- C. Epistaminal appendages deeply included.
- D. Anthers glabrous.
- E. Inflorescence much shorter than the subtending leaves; calyx-lobes 0.8–1.0 cm. long, only slightly suffused with purple at base and tip; corolla-tube gradually constricting toward the orifice; plants of Panama.....39. *P. versicolor*
- EE. Inflorescence about as long as the subtending leaves, or nearly so; calyx-lobes 1.1–1.5 cm. long, conspicuously and generally suffused with purple; corolla-tube not constricting toward the orifice; plants of Ecuador.....40. *P. peregrina*
- DD. Anthers minutely pubescent dorsally.
- E. Inflorescence dichotomous; plants of Colombia.....41. *P. vallis*
- EE. Inflorescence simple; plants of British Honduras.....42. *P. Schippii*
- CC. Epistaminal appendages exerted, or at least attaining the orifice.
- D. Calyx-lobes coriaceous to subcoriaceous; peduncle glabrous or very indefinitely papillate; species of Central America.
- E. Calyx-lobes 0.7–0.9 cm. long, obtusish to acute, scarcely if at all suffused with purple; squamellae acuminate; inflorescence twice to thrice dichotomous.....43. *P. guatemalensis*
- EE. Calyx-lobes 1.1–1.6 cm. long, acuminate, usually deeply suffused with purple; squamellae truncate, usually minutely erose; inflorescence once dichotomous to simple.....44. *P. portobellensis*

DD. Calyx-lobes membranaceous; peduncle densely and minutely ferruginous-puberulent; plants of eastern Peru.....45. *P. lacerata*

**14. *Prestonia exserta* (A. DC.) Standl.** Jour. Wash. Acad. Sci. **15**: 460. 1925.

*Haemadictyon exsertum* A. DC. in DC. Prodr. **8**: 426. 1844; Miers, Apoc. So. Am. 255. 1878.

*Prestonia tobagensis* Urb. Symb. Ant. **5**: 467. 1908.

*Prestonia gracilis* Rusby, Descr. So. Am. Pl. 91. 1920.

Stems relatively slender, softly puberulent when young, becoming glabrate and inconspicuously lenticellate when fully mature; leaves elliptic to broadly oval, acute to shortly acuminate, base obtuse to rounded, 6–12 cm. long, 2–6 cm. broad, membranaceous, either surface opaque, above glabrous, beneath minutely puberulent or glabrate to glabrous; petioles 0.6–1.5 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence corymbose, simple, bearing 10–40 yellow flowers; peduncle somewhat shorter than the subtending leaves, minutely puberulent to glabrate; pedicels 0.8–1.5 cm. long, somewhat accrescent after maturity, minutely puberulent; bracts linear to linear-lanceolate, 0.1–0.5 cm. long, only slightly foliaceous; calyx-lobes linear to linear-lanceolate, rarely oblong-elliptic, 0.6–0.7 cm. long, foliaceous, minutely puberulent without, the internal squamellae minutely lacerate; corolla salverform, glabrous or minutely papillate without, the tube 1.5–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages inserted at the base of the faucal annulus or slightly below, surpassing the anthers, 0.35–0.55 cm. long, the faucal annulus conspicuously thickened, the lobes broadly dolabriform, shortly acuminate to obtuse, 0.9–1.2 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, 0.45–0.55 cm. long, glabrous; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.12–0.2 cm. long; nectaries somewhat crescent at the base, compressed ovoid-oblongoid, about equaling the ovary; follicles relatively long and slender, somewhat agglutinated when young, eventually somewhat tortuous, 23–29 cm. long, glabrous; seeds 1.2–1.3 cm. long, the pale yellowish coma 2.2–2.7 cm. long.

PANAMA: COOLE: Penonome and vicinity, alt. 50-1000 ft., Febr. 23-March 22, 1908, *Williams 362* (NY); PANAMA: vine on shrubs on more or less forested slopes, Taboga Isl., Febr. 26-7, 1923, *Macbride 2785* (FM).

COLOMBIA: MAGDALENA: rare in forest, near Masinga, Nov. 18, 1898, *H. H. Smith 1644* (NY).

VENEZUELA: MERIDA: La Victoria, alt. 2000 ft., Nov. 21, 1856, *Fendler 2111* (G, MBG); ARAGUA: La Trinidad de Maracay, alt. 440 m., April 18, 1913, *Pittier 6047* (B); DISTRITO FEDERAL: Caracas, 1830, *Vargas 54* (DC, TYPE); in dry bushes, Puerto Escondido, March 2, 1930, *Pittier 13412* (US).

TRINIDAD: Erin, March 13, 1908, *Broadway 2730* (B); Belmont, Valley Road, Nov. 8, 1907, *Broadway 2840* (B); a climber on hedges, Botanic Station, Tobago, Dec. 6, 1909, *Broadway 3373* (B); Spring Road, Scarborough, Nov. 13, 1911, *Broadway 4150* (B, S, U); Welbeck, Tobago, Nov. 23, 1912, *Broadway 4350* (B, M); Knagg's Hill, Port of Spain, Nov. 20, 1921, *Williams 10966* (NY); Tobago prope "Frenchfield" in silvis interior., alt. 400 m., Oct. 23, 1889, *Eggers 5568* (B).

This species is manifestly not as uniform as others of the genus, but segregation has appeared inadvisable upon the basis of our present knowledge. *Williams 362*, from the northernmost known station of the species, is somewhat distinctive in its smaller size in general, and in the somewhat narrower leaves particularly. *Macbride 2785*, collected from not far distant, however, is typical in every obvious respect. The species as recognized above also varies in the pubescence of the leaves, the glabrous extreme being found, with obvious intergradations, upon the small island of Tobago, while the more pubescent are found upon the mainland in Venezuela. Although the type specimen of *P. gracilis* Rusby (*H. H. Smith 1644*) will fall into relationship with *P. exserta* in the key to species, its somewhat broader calyx-lobes suggest that it may represent a natural hybrid with the following species.

**15. *Prestonia velutina* Woodson, Ann. Mo. Bot. Gard. 18: 554. 1931.**

Stems relatively slender, persistently puberulent or pilosulose, apparently not lenticellate; leaves elliptic-lanceolate to broadly oval, apex acuminate, base obtuse, 5-7 cm. long, 2-4 cm. broad, membranaceous, above pilosulose to glabrate, beneath, densely and somewhat yellowish-tomentulose to minutely velutinous; petioles 0.5-1.5 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform-flagelliform; inflorescence corymbose, simple, bearing 10-15 greenish-yellow

flowers; peduncle somewhat shorter than the subtending leaves, shortly hirtellous or pilosulose; pedicels 1.0–1.4 cm. long, somewhat accrescent after maturity, pubescence as on the peduncle; bracts elliptic to obovate-lanceolate, 0.7–1.0 cm. long, conspicuously foliaceous, minutely puberulent; calyx-lobes oblong-lanceolate, acute to acuminate, 1.0–1.2 cm. long, foliaceous, minutely puberulent without, the internal squamellae deltoid-ligular, minutely erose; corolla salverform, glabrous without, the tube 1.6–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages inserted at the base of the faucal annulus or slightly below, surpassing the anthers, 0.45–0.55 cm. long, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, 0.5 cm. long, glabrous; ovary ovoid, about 0.2 cm. long; stigma 0.15 cm. long; nectaries fleshy, more or less conerescent, somewhat shorter than the ovary; follicles unknown.

COLOMBIA: MAGDALENA: Aracataca, alt. 30 m., Dec. 25, 1925, *Schultze 245* (B); CUNDINAMARCA: moist open loam, alt. 350–400 m., Girardot, July 19, 1917, *Eusby & Pennell 121* (G, NY); Girardot, Febr. 15, 1929, *Toro 59* (NY); TOLIMA: Honda, Aug., 1919, *Ariste-Joseph s.n.* (NY, TYPE, MBG, photograph and analytical drawings).

This species is somewhat intermediate between *P. exserta* and *P. parvifolia*, of which it may conceivably be a hybrid, although it is evidently rather stable in its morphology, and extends without the known range of the former species, except to the north, and is even further removed from the latter to the south in Ecuador.

**16. *Prestonia parvifolia* K. Sch. spec. nov. in herb.**

Suffrutescens volubilis; ramulis gracilibus juventate pilosulis hirtellisve tandem glabratis haud conspicue lenticellatis; foliis ovalibus obovato-ellipticisve apice breviter acuminatis basi obtusis 5–7 cm. longis 2–4 cm. latis membranaceis opacis supra minute sparseque strigilloso-hirtellis subtus minute puberulis; petiolis 0.4–0.6 cm. longis puberulis; appendicibus stipulaceis intrapetiolearibus numerosis minute dentiformibus;

inflorescentiis corymbosis simplicibus 15–30-floris; pedunculo foliis brevior hirtello; pedicellis 0.7–1.0 cm. longis puberulis; bracteis obovato-ellipticis 0.7–1.0 cm. longis foliaceis sparse minuteque puberulo-papillatis; calycis laciniis obovato-ellipticis brevissime acuminatis 1.1–1.4 cm. longis foliaceis minute sparseque puberulo-papillatis squamellis deltoideis minute erosis; corollae salverformis virido-luteae extus sparse minuteque puberulo-papillatae tubo 1.6–1.8 cm. longo basi ca. 0.4 cm. diametro metiente appendicibus epistaminalibus paulo exsertis 0.25–0.3 cm. longis multo brevioribus quam antheris annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.9–1.0 cm. longis reflexis patulisve; antheris oblongo-sagittatis 0.5–0.55 cm. longis glabris; ovario ovoideo ca. 0.2 cm. longo glabro; stigmatibus 0.15–0.16 cm. longo; nectariis compresse oblongoideis basi plus minusve concrecentibus ovario paululo brevioribus; folliculis ignotis.

Stems relatively slender, pilosulose or hirtellous when young, glabrate but not conspicuously lenticellate when fully mature; leaves oval to obovate-elliptic, apex shortly acuminate, base obtuse, 5–7 cm. long, 2–4 cm. broad, membranaceous, opaque, above minutely and sparsely strigillose-hirtellous, beneath minutely puberulent; petioles 0.4–0.6 cm. long, puberulent; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence corymbose, simple, bearing 15–30 yellow flowers; peduncle somewhat shorter than the subtending leaves, hirtellous; pedicels 0.7–1.0 cm. long, somewhat accrescent after maturity, puberulent; bracts obovate-elliptic, 0.7–1.0 cm. long, conspicuously foliaceous, minutely and sparsely puberulent-papillate; calyx-lobes obovate-elliptic, very shortly acuminate, 1.1–1.4 cm. long, foliaceous, minutely and sparsely puberulent-papillate, the internal squamellae deltoid, minutely erose; corolla salverform, minutely puberulent-papillate without, the tube 1.6–1.8 cm. long, about 0.4 cm. in diameter at the base, epistaminal appendages slightly exserted, much surpassed by the anthers, 0.25–0.3 cm. long, the faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.9–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers



oblong-sagittate, 0.5–0.55 cm. long, glabrous; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.15–0.16 cm. long; nectaries compressed-oblongoid, somewhat concrescent at the base, slightly shorter than the ovary; follicles unknown.

ECUADOR: MANABI: prope Hacienda El Recreo, May 6, 1895, *Eggers 15430* (B, TYPE, MBG, photograph and analytical drawings); in locis siccis, El Recreo, Sept., 1893, *Eggers 15430 bis* (M); GUAYAS: "Fl. Huayaquil," date lacking, *Pavon s.n.* (BB).

Similar to *P. velutina* in the approximate shape and size of the bracts and calyx-lobes, but differing notably in the shorter, barely exerted epistaminal appendages, more floriferous inflorescences, and puberulent-papillate corolla.

**17. *Prestonia perplexa* Woodson, spec. nov.**

Suffruticosa vel suffrutescens volubilis; ramulis gracilibus juventate minute hirtellis tandem glabratis inconspicue lenticellatis cortice rubro-brunneo; foliis ovato-ellipticis apice acuminatis basi obtusis 6–10 cm. longis 3–6 cm. latis rigide membranaceis supra juventate minutissime puberulis mox glabratis subtus glabris; petiolis 0.8–1.0 cm. longis glabris; appendicibus stipulaceis interpetiolaribus numerosis minute angustequae dentiformibus; inflorescentiis subcorymbosis simplicibus 12–20-floris; pedunculo foliis subaequante vel paulo superante minute hirtello; pedicellis 1.2–1.5 cm. longis post maturitatem conspicue accrescentibus minute hirtellis; bracteis linearibus 0.1–0.4 cm. longis paululo foliaceis; calycis laciniis late obovato-ellipticis acutis acuminatisve 0.8–1.1 cm. longis foliaceis sparse indistinctequae puberulo-papillatis squamellis late deltoideis minute emarginatis vel erosis; corollae salverformis dilute virido-luteae extus sparse minutissimeque papillatae tubo 1.3–1.5 cm. longo basi ca. 0.3 cm. diametro metiente appendicibus epistaminalibus haud vel vix exsertis 0.2–0.25 cm. longis multo brevioribus quam antheris annulo faucium conspicue incrassato lobis obovato-dolabriformibus haud acuminatis 0.6–0.8 cm. longis patentibus; antheris exsertis sagittatis 0.45 cm. longis glabris; ovario ovoideo ca. 0.1 cm. longo minutissime papillato; stigmate 0.175–0.2 cm. longo; nectariis com-

presse ovoideis basi connatis ovarium aequantibus; folliculis ignotis.

Stems relatively slender, minutely hirtellous when young, becoming glabrate and very inconspicuously lenticellate with a reddish-brown bark; leaves ovate-elliptic, apex acuminate, base obtuse, 6–10 cm. long, 3–6 cm. broad, firmly membranaceous, above very minutely puberulent when young, soon becoming glabrate, beneath glabrous; petioles 0.8–1.0 cm. long, glabrous; stipular appendages interpetiolar, minutely and narrowly dentiform; inflorescence subcorymbose, simple, bearing 12–20 pale greenish-yellow flowers; peduncle about equalling or slightly surpassing the subtending leaves, minutely hirtellous; pedicels 1.2–1.5 cm. long, conspicuously accrescent after maturity, minutely hirtellous; bracts linear, 0.1–0.4 cm. long, only slightly foliaceous; calyx-lobes broadly obovate-elliptic, acute to acuminate, 0.8–1.1 cm. long, conspicuously foliaceous, membranaceous, sparsely and indistinctly puberulent-papillate, the squamellae broadly deltoid, minutely emarginate or erose; corolla salverform, sparsely and very minutely papillate without, the tube 1.3–1.5 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages barely exerted or essentially included, much surpassed by the anthers, 0.2–0.25 cm. long, faucal annulus conspicuously thickened, the lobes obovate-dolabriform, not acuminate, 0.6–0.8 cm. long, reflexed or widely spreading; anthers inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, sagittate, 0.45 cm. long, glabrous, the tips conspicuously exerted; ovary ovoid, about 0.1 cm. long, very minutely papillate; stigma 0.175–0.2 cm. long; nectaries compressed-ovoid, united at the base, fleshy, about equalling the ovary; follicles unknown.

BRAZIL: DATA INCOMPLETE: *Lund s.n.* (C, TYPE, MBG, photograph and analytical drawings).

It is obviously dangerous, as well as exasperating, to base a species upon a single collection bearing no data but the name of the collector and merely the notation "Brasilia." Nevertheless, a taxonomic monograph is obliged to consider all material available however scanty and dubious as to origin. As the

majority of Brazilian Apocynaceae collected by Lund and bearing more exact data have been from the southeastern coastal states, it appears that the provenience of the type specimen of *P. perplexa* may rather safely be assigned to that general region, the states of Rio de Janeiro or São Paulo in particular.

The morphological characters of *P. perplexa* indicate a strong relationship to *P. parvifolia* of Ecuador, and to no other known species of its own regional flora. From the latter species, however, *P. perplexa* is amply distinct in such characters as the dimensions of the flower as well as those employed in the key.

**18. *Prestonia mollis* HBK. Nov. Gen. 3: 221. 1819.**

*Prestonia glabrata* HBK. loc. cit. 222. 1819; Miers, Apoc. So. Am. 145. 1878, not K. Sch.

*Haemadictyon molle* (HBK.) A. DC. in DC. Prodr. 8: 427. 1844.

*Haemadictyon glabratum* (HBK.) A. DC. loc. cit. 1844.

*Haemadictyon pallidum* A. DC. loc. cit. 428. 1844; Miers, loc. cit. 259. 1878.

*Haemadictyon tomentellum* Benth. Bot. Voy. Sulph. 126. 1844; Miers, loc. cit. 1878.

*Prestonia ecuadorensis* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895.

*Prestonia Weberbaueri* Mgf. Notizblatt 9: 89. 1924.

Stems relatively slender, usually minutely puberulent or puberulent-papillate when young, soon becoming glabrate and rather conspicuously lenticellate; leaves broadly ovate to oblong-elliptic, apex shortly and abruptly acuminate to obtuse or rounded, base usually broadly and rather obscurely cordate to rounded or somewhat truncate, 4–15 cm. long, 2–9 cm. broad, membranaceous, above minutely and rather sparsely puberulent-papillate to glabrate or glabrous, beneath minutely tomentulose to glabrate or glabrous, usually paler and somewhat glaucescent; petioles 0.5–3.5 cm. long, minutely and rather sparsely puberulent-papillate to glabrate or glabrous; stipular appendages intrapetiolar, numerous, minutely dentiform-fla-

gelliform; inflorescence corymbose, simple, bearing 10–40 pale yellow flowers; peduncle somewhat shorter than the subtending leaves, very minutely puberulent to glabrous; pedicels 0.6–1.2 cm. long, somewhat accrescent after maturity, minutely puberulent to glabrous; bracts narrowly oblong-lanceolate, acuminate, 0.5–2.6 cm. long, conspicuously foliaceous, minutely papillate to glabrous; calyx-lobes narrowly oblong-lanceolate to linear, acuminate, 0.8–2.1 cm. long, conspicuously foliaceous, minutely papillate to glabrous without, the internal squamellae deltoid, minutely erose or lacerate; corolla salverform, glabrous or minutely papillate without, 2.2–3.4 cm. long, 0.4–0.5 cm. in diameter at the base, epistaminal appendages slightly exserted or at least attaining the orifice, 0.2–0.55 cm. long, the faucal annulus conspicuously thickened, the lobes obliquely obovate, usually shortly acuminate, occasionally obtuse, 1.7–2.5 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers narrowly sagittate, 0.6–0.8 cm. long, minutely hirtellous, rarely nearly glabrate, slightly exserted; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.15–0.2 cm. long; nectaries compressed-ovoid, separate or essentially so, about half equalling the ovary; follicles relatively stout, continuous, usually agglutinated and joined at the tips, 15–30 cm. long, glabrous; seeds 0.8–1.0 cm. long, the pale yellowish coma 3.5–4.0 cm. long.

EQUADOR: MANABI: prope Hacienda El Recreo, Aug. 4, 1893, *Eggers 14956* (B, M); GUAYAS: Insula Puna, May, 1892, *Eggers 14782* (B, M); prope Guayaquil, date lacking, *Sodiro s.n.* (B); on Puna, 1852, *Andersson 79* (S); Guayaquil, 1852, *Andersson 79* (S); Guayaquil, date lacking, *Hartweg 670* (Camb., V); ad fluvium Daule prope Guayaquil, date lacking, *Spruce 6484* (B, BB, DL, V); oil camp between Guayaquil and Salinas, alt. 0–100 m., June 21–24, 1923, *Hitchcock 20069* (G, NY, US); Panigon Plantation, 8 miles south of Milagro, alt. 50 m., July 11–13, 1923, *Hitchcock 20593* (G, NY, US); DATA INCOMPLETE: *Warszewicz s.n.* (B); in *Andibus Ecuadorensibus*, 1857–9, *Spruce 6019* (BB, DC, DL, G, V).

PERU: AMAZONAS: Chachapoyas, 1862, *Matthews s.n.* (BB, NY); am Marañon bei Balsas, Uhrgehölz, gemischt aus Bäumen, Sträuchern, und hohen Rohrgräsern, alt. 920 m., June 24, 1904, *Weberbauer 4265* (B); CAJAMARCA: Tal des Marañon bei Bellavista, Regengrünes Gebüsch, gebildet aus hohen Sträuchern und kleinen Bäumen, alt. 500–600 m., Mai 2, 1912, *Weberbauer 6231* (B, G).

The specimens from northern Peru, representing roughly *P. Weberbaueri* Mgf., appear to be distinguished superficially

from the more typical specimens from farther north in having somewhat smaller leaves with less indication of the obscurely cordate base. However, enlisting all the specimens cited above in a rather uniform series of intergradations, it will be found that the extremes have been collected in the province of Guayas, Ecuador, alone. The type specimen of *P. Weberbaueri* (Weberbauer 6231 in herb. Berol.) is also distinguished by anthers approaching glabrescence. This character, however, is not shared by other specimens from Peru. Seen separately, the specimens cited appear to indicate need of segregation: when examined altogether, the unity of the species is apparent.

19. *Prestonia didyma* (Vell.) Woodson, comb. nov.

*Echites didyma* Vell. Fl. Flum. 109. 1830; Icon. 3: pl. 27. 1827; A. DC. in DC. Prodr. 8: 468. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 155. 1860.

*Haemadictyon membranaceum* Muell.-Arg. loc. cit. 167. 1860; Miers, Apoc. So. Am. 260. 1878.

*Rhaptocarpus didymus* (Vell.) Miers, loc. cit. 152. 1878.

Stems relatively stout, puberulent when young, glabrate and inconspicuously lenticellate when fully mature; leaves ovate-elliptic to rather narrowly oval, apex acuminate, base obtuse, 9–16 cm. long, 3.0–8.5 cm. broad, membranaceous, glabrous; petioles 1–2 cm. long; stipular appendages intrapetiolar, numerous, very minutely dentiform; inflorescence racemose, simple, bearing 10–20 rather livid greenish-yellow flowers; peduncle somewhat shorter than the subtending leaves, minutely puberulent; pedicels 1.5–2.1 cm. long, somewhat accrescent after maturity, minutely puberulent; bracts linear, 0.3–0.4 cm. long, very slightly foliaceous; calyx-lobes elliptic-lanceolate, acuminate, 1.2–1.8 cm. long, green, faintly flushed with purple toward the base, glabrous, the internal squamellae deltoid-trigonal, minutely emarginate or erose; corolla salverform, glabrous or minutely papillate without, the tube 0.8–1.5 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages wholly included, about 0.2 cm. long, the faucal annulus conspicuously thickened, the lobes obliquely obovate,

0.75–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers very narrowly sagittate, about 0.6 cm. long, glabrous, slightly exserted; ovary ovoid, about 0.1 cm. long, glabrous; stigma 0.15 cm. long; nectaries compressed-ovoid, conspicuously concrescent at the base, somewhat surpassing the ovary; follicles relatively stout, continuous, usually united at the tips and somewhat agglutinated, 20–25 cm. long, glabrous; seeds 1.0–1.1 cm. long, the pale yellowish coma 3.0–3.5 cm. long.

BRAZIL: RIO GRANDE DO NORTE: Taipu, date lacking, *Schott 5389* (V, TYPE, MBG, photograph and analytical drawings); RIO DE JANEIRO: ad urbem loco Fortaleza São João, March 25, 1916, *Frasão 7144* (B); DATA INCOMPLETE: *Sellow s.n.* (B).

The foundation of this transfer appears to be well established through a technical examination of Velloso's plate of a plant collected "in sylvis maritimis" in the vicinity of Rio de Janeiro. Velloso's illustrations, although often almost comically wooden and lifeless, frequently portray with surprising aptitude basic characteristics of the species depicted. In this respect they may be comparable to modern "cartoons."

20. *Prestonia annularis* (L. f.) G. Don, Gen. Hist. 4: 84. 1838.

*Echites annularis* L. f. Suppl. 166. 1781.

*Haemadictyon ? annulare* (L. f.) A. DC. in DC. Prodr. 8: 428. 1844.

*Temnadenia annularis* (L. f.) Miers, Apoc. So. Am. 216. 1878.

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves broadly ovate to oblong-elliptic, apex obtuse to acute, base obtuse to rounded, 14–27 cm. long, 4.5–12.0 cm. broad, subcoriaceous, opaque; petioles 0.7–2.0 cm. long; stipular appendages intra- or interpetiolar, numerous, minutely dentiform-flagelliform; inflorescence racemose, dichotomous, bearing 10–30 purplish-yellow flowers; peduncle much shorter than the subtending leaves; pedicels 1.1–1.3 cm. long, somewhat accrescent after maturity; bracts linear, about 0.1 cm. long, scarious or only slightly foliaceous; calyx-lobes oblong-elliptic, acute to acuminate, 0.7–1.0 cm. long, subcoriaceous, pale green suffused with purple, gla-

brous without, the internal squamellae deltoid-ligular, minutely erose or truncate; corolla salverform, glabrous or very minutely papillate without, the tube 1.3–1.5 cm. long, about 0.25 cm. in diameter at the base, epistaminal appendages wholly included, about 0.15 cm. long, the faucal annulus conspicuously thickened, the lobes obliquely obovate-dolabriform, 0.8–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers oblong-sagittate, 0.45–0.5 cm. long, minutely puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.1 cm. long, glabrous; stigma 0.1–0.15 cm. long; nectaries compressed-ovoid, separate or somewhat conrescent at the base, about equalling the ovary; follicles relatively long and stout, continuous, usually somewhat falcate and frequently united at the tips, 40–45 cm. long, glabrous; seeds 1.2–1.4 cm. long, the pale yellowish coma 3.5–4.0 cm. long.

DUTCH GUIANA: e regione Para, 1851, *Wulfschlägel 1028* (Bx); Jaglust, fluv. Suriname, in silva, June 26, 1913, *Alprato 40E* (U); Paramaribo, date lacking, *Focke 1056* (U); Paramaribo, June 25, 1850, *Wulfschlägel 1028* (U, V); data incomplete, *Hostmann & Kappler s.n.* (S).

**21. *Prestonia guianensis* Gleason, Bull. Torrey Bot. Club 53: 299. 1926.**

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves oval to oblong-elliptic, apex acuminate, base obtuse to rounded, 10–13 cm. long, 4.5–6.0 cm. broad, subcoriaceous, opaque; petioles 0.7–1.0 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence racemose, dichotomous, bearing 30–40 cream-colored flowers; peduncle equalling or somewhat surpassing the subtending leaves; pedicels 0.8–1.0 cm. long, somewhat accrescent after maturity; bracts linear, scarious, less than 0.1 cm. long; calyx-lobes oblong-elliptic, acute to acuminate, membranaceous or nearly subcoriaceous, 0.9–1.0 cm. long, green suffused with purple, the internal squamellae broadly deltoid-dentiform, truncate or very minutely erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.2–1.4 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages wholly included, about 0.07–0.1

cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 1.0–1.25 cm. long; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers elliptic-sagittate, 0.5–0.55 cm. long, puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.1 cm. long, glabrous; stigma 0.08–0.1 cm. long; nectaries compressed-ovoid, separate or slightly conrescent at the base, equalling the ovary; follicles unknown.

BRITISH GUIANA: Pomeroon River, Pomeroon District, Dec. 17–24, 1922, *Cruz 3097* (G, NY, TYPE, MBG, photograph and analytical drawings).

Although this species is closely related to *P. annularis* of adjoining Dutch Guiana, it seems distinct because of its thicker foliage, as well as its longer corolla-lobes which appear nearly white, and longer inflorescence with longer floriferous branches and shorter sterile primary peduncle.

**22. *Prestonia purpurissata* Woodson, spec. nov.**

Suffruticosa volubilis; ramulis crassiusculis maturitate glabris conspicue lenticellatis; foliis ovalibus oblongo-ellipticisve apice breviter acuminatis obtusisve basi obtusis vel rotundatis 9–15 cm. longis 3.0–6.5 cm. latis firme membranaceis opacis omnino glabris; petiolis 0.5–1.0 cm. longis; appendicibus stipulaceis interpetiolaribus numerosis minute dentiforme-flagelliformibus; inflorescentiis subcorymbosis di- vel trichotome divisae flores 20–40 purpurissatos gerentibus; pedunculo foliis subaequante; pedicellis 1.3–1.5 cm. longis post maturitatem paulo accrescentibus minutissime papillatis; bracteis linearibus 0.1–0.4 cm. longis scariaceis; calycis laciniis oblongo-lanceolatis acuminatis 1.7–1.8 cm. longis membranaceis sat purpurissatis squamellis dentiformibus emarginatis vel paulo laceratis; corollae salverformis extus glabrae vel minutissime papillatae tubo 1.7–1.9 cm. longo basi ca. 0.35 cm. diametro metiente appendicibus epistaminalibus omnino inclusis ca. 0.1 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis acuminatis 1.0–1.2 cm. longis patentibus; antheris pandurate sagittatis 0.6 cm. longis dorso minute papillatis paulo exsertis; ovario ovoideo ca. 0.2 cm. longo glabro; stigmatibus ca. 0.15 cm. longo; nectariis compresse oblongoideis integris vel basi paul-



lulo concretescentibus ovarium paulo superantibus; folliculis ignotis.

Plants completely glabrous; stems relatively stout, glabrous and conspicuously lenticellate when fully mature; leaves oval to oblong-elliptic, apex obtuse or shortly acuminate, base obtuse or rounded, 9–15 cm. long, 3.0–6.5 cm. broad, firmly membranaceous, opaque; petioles 0.5–1.0 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform-flagelliform; inflorescence subcorymbose, di- or trichotomous, bearing 20–40 “raisin-purple” flowers; peduncle about equalling the subtending leaves; pedicels 1.3–1.5 cm. long, somewhat accrescent after maturity, very minutely papillate; bracts linear, 0.1–0.4 cm. long, scarious; calyx-lobes oblong-lanceolate, acuminate, 1.7–1.8 cm. long, membranaceous, conspicuously flushed with purple, the internal squamellae dentiform, emarginate or slightly erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.7–1.9 cm. long, about 0.35 cm. in diameter at the base, epistaminal appendages wholly included, about 0.1 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, acuminate, 1.0–1.2 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers sagittate, somewhat pandurate, 0.6 cm. long, minutely papillate dorsally, slightly exserted; ovary ovoid, about 0.2 cm. long, glabrous; stigma about 0.15 cm. long; nectaries compressed-oblongoid, separate or somewhat concrescent at the base, slightly surpassing the ovary; follicles unknown.

COLOMBIA: EL VALLE: edge of forest, La Cumbre, alt. 1650–1850 m., May 14–19, 1922, Pennell 5719 (US, TYPE, MBG, photograph and analytical drawings).

Differs from its immediate relatives, *P. finitima* and *P. Phenax* superficially in its longer, delicately petalaceous calyx-lobes.

### 23. *Prestonia finitima* Woodson, spec. nov.

Suffruticosa volubilis; ramulis crassiusculis juventate minute puberulis maturitate glabratis inconspicueque lenticellatis; foliis ellipticis apice acuminatis basi obtusis 9–25 cm. longis 3.0–11.0 cm. latis tenuiter membranaceis opacis juven-

tate minute sparseque puberulis mox glabratis; petiolis 1.3–2.5 cm. longis; appendicibus stipulaceis interpetiolaribus minute dentiforme-flagelliformibus; inflorescentiis subcorymbosis dichotome divisis flores 15–20 lutescentes gerentibus; pedunculo foliis paulo brevior; pedicellis 1.4–1.5 cm. longis, post maturitatem paulo accrescentibus indistincte papillatis; bracteis minutissimis vix bene visis; calycis laciniis late oblongo-ellipticis breviter acuminatis 1.2–1.4 cm. longis subcoriaceis purpurissatis glabris vel indistinctissime papillatis squamellis latissime deltoideis erosis; corollae salverformis extus indistincte papillatae tubo 1.8–1.9 cm. longo basi ca. 0.4 cm. diametro metiente prope fauces sensim angustato appendicibus epistaminalibus omnino inclusis ca. 0.1 cm. longis anulo faucium conspicue incrassato lobis oblique-obovatis breviter acuminatis 0.7–1.0 cm. longis patentibus; antheris pandurate sagittatis 0.5 cm. longis dorso puberulo-papillatis paulo exsertis; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus 0.15–0.2 cm. longo; nectariis compresse-oblongoideis ovarium paulo superantibus prope basem connatis apice truncatis vel leviter undulatis; folliculis ignotis.

Stems relatively stout, minutely puberulent when young, glabrate and inconspicuously lenticellate when fully mature; leaves elliptic, apex acuminate, base obtuse, 9–25 cm. long, 3.0–11.0 cm. broad, delicately membranaceous, minutely and sparsely puberulent when young, soon becoming glabrate; petioles 1.3–2.5 cm. long, glabrous; stipular appendages interpetiolar, numerous, minutely dentiform-flagelliform; inflorescence subcorymbose, dichotomous, bearing 15–20 brownish-yellow flowers; peduncle somewhat shorter than the subtending leaves, glabrous; pedicels 1.4–1.5 cm. long, somewhat accrescent after maturity, indistinctly papillate; bracts very minute, scarcely visible; calyx-lobes broadly oblong-elliptic, shortly acuminate, 1.2–1.4 cm. long, subcoriaceous, suffused with purple, glabrous or very indistinctly papillate, the internal squamellae very broadly deltoid, erose; corolla salverform, indistinctly papillate without, the tube 1.8–1.9 cm. long, about 0.4 cm. in diameter at the base, gradually constricting toward the orifice, epistaminal appendages wholly included, about 0.1

cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers pandurately sagittate, 0.5 cm. long, puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15–0.2 cm. long; nectaries compressed-oblongoid, slightly surpassing the ovary, connate toward the base, the apices truncate or slightly undulate; follicles unknown.

BRAZIL: AMAZONAS: Suhinya, Sept. 1, 1912, *Koch-Gruenberg 30* (B, TYPE, MBG, photograph and analytical drawings); Municipality Humayta, near Tres Casas, on varzea land, Sept. 14–Oct. 11, 1934, *Krukoff 6190* (NY).

There is a very obvious danger in depending too trustingly upon collectors' notes concerning flower color in the majority of cases, without doubt. In the instance of the species centering about *P. Phenax* and *P. trifida*, however, the collector's report of the flower color has been found to coincide with certain morphological characters used in the delimitation of species. Furthermore in the case of species represented by several specimens with flower color noted, sufficient unanimity has been found to use such observations in descriptions, and to a less extent in keys. It is thought that such notes may be of use in identification, particularly when fresh material may be available.

#### 24. *Prestonia Phenax* Woodson, spec. nov.

Suffruticosa volubilis; ramulis crassiusculis maturitate glabris conspicue lenticellatis; foliis late ovatis vel late oblongo-ellipticis apice acuminatis rariusve obtusiusculis basi obtusis vel rotundatis 10–28 cm. longis 4–14 cm. latis subcoriaceis opacis glabris; petiolis 0.8–2.0 cm. longis glabris; appendicibus stipulaceis interpetiolaribus numerosis minute dentiformibus; inflorescentiis corymbosis di- vel trichotome divisus flores viridi-luteos 10–30 gerentibus; pedunculo foliis multo brevior; pedicellis 1.0–1.3 cm. longis glabris post maturitatem paulo accrescentibus; bracteis linearibus minutis vix bene visis; calycis laciniis oblongo-ellipticis apice acutis vel breviter acuminatis 1.2–1.3 cm. longis membranaceis vel subcoriaceis

viridibus basi apiceque purpurissatis glabris squamellis late deltoideis minute emarginatis integrisve; corollae salverformis extus glabrae vel minutissime papillatae tubo 1.5–1.7 cm. longo basi ca. 0.3–0.4 cm. diametro metiente appendicibus epistaminalibus omnino inclusis ca. 0.1–0.2 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.8–1.2 cm. longis patentibus; antheris sagittatis paulo panduratis 0.5 cm. longis dorso minute puberulo-papillatis paulo exsertis; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus 0.15–0.2 cm. longo; nectariis compresse oblongo-ovoideis integris vel basi conerescentibus ovarium paulo superantibus; folliculis juventate gracilibus continuis falcatis apice connatis; seminibus ignotis.

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves broadly ovate to oblong-elliptic, apex acuminate to somewhat obtuse, base obtuse or rounded, 10–28 cm. long, 4–14 cm. broad, subcoriaceous, opaque; petioles 0.8–2.0 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose, di- or trichotomous, bearing 10–30 greenish-yellow, brown-tinted flowers; peduncle much shorter than the subtending leaves; pedicels 1.0–1.3 cm. long, somewhat accrescent after maturity; bracts linear, minute, very inconspicuous; calyx-lobes oblong-elliptic, acute or shortly acuminate, 1.2–1.3 cm. long, membranaceous or subcoriaceous, green tinted with purple at base and tip, glabrous, the internal squamellae broadly deltoid, entire or minutely emarginate; corolla salverform, glabrous or minutely papillate without, the tube 1.5–1.7 cm. long, about 0.3–0.4 cm. in diameter at the base, epistaminal appendages wholly included, 0.1–0.2 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8–1.2 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers oblong-sagittate, somewhat pandurate, 0.5 cm. long, minutely puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15–0.2 cm. long; nectaries compressed oblong-ovoid, separate or somewhat united at the base,

somewhat surpassing the ovary; immature follicles relatively slender, continuous, falcate, united at the apex; seeds unknown.

PERU: LORETO: Urwald, Stromgebiet des Ucayali von 10° S. bis zur Mündung, July 26, 1923, *Tessmann 3046* (B, TYPE, MBG, photograph and analytical drawings); edge of water, Fortaleza, Yurimaguas, Oct.-Nov., 1929, *Williams 4310* (B, FM).

BOLIVIA: SANTA CRUZ: barranca en el bosque, Rio Surutu, alt. 400 m., Oct. 8, 1925, *Steinbach 7272* (B).

*Williams 4310* may be found to represent another species or variety, since it differs from the other specimens cited in having somewhat smaller, narrower leaves, and more conspicuously purplish calyx. *Tessmann 3046* and *Steinbach 7272* from widely separate localities, however, show striking uniformity in all observable characters.

**25. *Prestonia Brittonii* N. E. Br. Bull. Torrey Bot. Club 51: 5. 1924.**

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves oval, apex shortly acuminate, base obtuse or rounded, 13-16 cm. long, 7-9 cm. broad, rigidly membranaceous to subcoriaceous, opaque; petioles 1.5-2.5 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform-flagelliform; inflorescence corymbose, repeatedly dichotomous, bearing 40-50 brownish-yellow flowers; peduncle much surpassing the subtending leaves; pedicels 1.7-2.1 cm. long, somewhat accrescent after maturity; bracts minutely ovate-lanceolate, very inconspicuous; calyx-lobes oblong-elliptic, apex acute to shortly acuminate, 1.0-1.25 cm. long, subcoriaceous, deep purple, glabrous or very indistinctly papillate, the internal squamellae broadly deltoid, minutely erose; corolla salverform, glabrous without, the tube 1.5-1.8 cm. long, about 0.35 cm. in diameter at the base, very slightly constricting toward the orifice, epistaminal appendages deeply included, 0.15 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8-0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers oblong-sagittate, somewhat pandurate, 0.5 cm. long,

minutely puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.1 cm. long, glabrous; stigma 0.15 cm. long; nectaries compressed-oblongoid, separate or slightly conrescent at the base, apex truncate or minutely emarginate, equaling or slightly surpassing the ovary; follicles unknown.

TRINIDAD: Heights of Aripo, Jan. 10-26, 1922, *Broadway 10009* (NY, *ISOTYPE*, MBG, photograph and analytical drawings).

**26. *Prestonia laxa* Rusby, spec. nov. in herb.**

Suffruticosa volubilis; ramulis gracilibus juventate minute sparseque puberulis maturitate glabratis inconspicue lenticellatis; foliis oblongo-ellipticis apice breviter acuminatis basi obtusis rotundatisve 9-19 cm. longis 2.7-7.5 cm. latis rigide membranaceis vel subcoriaceis opacis vel supra paululo nitidulis; petiolis 0.5-0.8 cm. longis; appendicibus stipulaceis interpetiolaribus numerosis minute dentiformibus; inflorescentiis corymbosis dichotome subdivisis flores 10-40 albidos carneo-maculatos gerentibus; pedunculo folia multo superante; pedicellis 1.5-2.0 cm. longis post maturitatem paulo acrescentibus minutissime papillatis; bracteis linearibus 0.1-0.2 cm. longis scariaceis; calycis laciniis oblongo-ellipticis apice breviter acuminatis 1.0-1.4 cm. longis tenuiter membranaceis viridi-purpurissatis extus glabris vel minutissime papillatis squamellis dentiforme-trigonalibus; corollae salverformis extus glabrae tubo 1.8-2.3 cm. longo basi ca. 0.4 cm. diametro metiente appendicibus epistaminalibus paulo exsertis ca. 0.5 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.7-0.8 cm. longis patentibus; antheris oblongo-sagittatis paulo panduratis 0.5-0.55 cm. longis dorso minute puberulo-papillatis paulo exsertis; ovario ovoideo ca. 0.2 cm. longo glabro; stigmatibus 0.15 cm. longo; nectariis compresse ovoideis integris vel basi plus minusve connatis ovario brevioribus; folliculus juventate gracilibus continuis falcatis glabris; seminibus ignotis.

Stems relatively slender, sparsely and minutely puberulent when young, glabrate and inconspicuously lenticellate when fully mature; leaves oblong-elliptic, apex shortly acuminate, base obtuse to rounded, 9-19 cm. long, 2.7-7.5 cm. broad, rigidly

membranaceous to subcoriaceous, opaque or somewhat nitidulous above, glabrous; petioles 0.5–0.8 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose, dichotomously subdivided, bearing 10–40 white, crimson-blotched flowers; peduncle much surpassing the subtended leaves; pedicels 1.5–2.0 cm. long, somewhat accrescent after maturity, minutely papillate; bracts linear, 0.1–0.2 cm. long, scarious; calyx-lobes oblong, elliptic, shortly acuminate, 1.0–1.4 cm. long, delicately membranaceous, greenish-purple, glabrous or very minutely papillate without, the internal squamellae dentiform-trigonal; corolla salverform, glabrous without, the tube 1.8–2.3 cm. long, about 0.4 cm. in diameter at the base, epistaminal appendages slightly exserted, about 0.5 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–0.8 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, slightly pandurate, 0.5–0.55 cm. long, minutely puberulent-papillate dorsally, slightly exserted; ovary ovoid, about 0.2 cm. long, glabrous; stigma about 0.15 cm. long; nectaries compressed-ovoid, separate or somewhat connate at the base, somewhat shorter than the ovary; immature follicles relatively slender, continuous, falcate, glabrous; seeds unknown.

COLOMBIA: MAGDALENA: edge of mountain forest and clearing below Valparaiso, alt. 4000 ft., March 26, 1899, *H. H. Smith 1647* (NY, TYPE, G, MBG, photograph and analytical drawings); Bergenwald, Sierra Nevada de Santa Marta, July 9, 1926, *Schultze 474* (B).

The color of the corolla is described by Smith as "whitish blotched with crimson around the throat," and by Schultze as "rotlich weiss, innen schneeweiss dunkelkarmin rot gezeichnet. Der Ring goldgelb."

**27. *Prestonia rotundifolia* K. Sch. spec. nov. in herb.**

Suffruticosa volubilis; ramulis juventate minute puberulis maturitate glabratis conspicue lenticellatis; foliis late ovalibus vel late obovato-ovalibus apice obtusis rotundatisve saepius minute mucronatis basi rotundatis 9.5–17.5 cm. longis 4.5–10.0 cm. latis rigide membranaceis opacis glabris; petiolis 0.6–1.6

cm. longis glabris; appendicibus stipulaceis intrapetiolaribus multis minute dentiforme-flagelliformibus; inflorescentiis corymbosis subumbellatis obscure di- vel trichotome divisas flores 8–20 luteos gerentibus; pedunculo foliis multo brevior; pedicellis 1.1–1.2 cm. longis minute appressequ puberulis; bracteis anguste elliptico-oblongeolatis 0.65–1.2 cm. longis plus minusve petalaceis purpurissatis caducis; calycis laciniis oblongo-ellipticis breviter acuminatis 0.9–1.1 cm. longis subcoriaceis purpurissatis extus minutissime appressequ puberulo-papillatis squamellis dentiforme-deltoides minutissime eros; corollae salverformis extus minute papillatae tubo 1.5–1.7 cm. longo basi ca. 0.35 cm. diametro metiente appendicibus epistaminalibus faucibus paene attingentibus ca. 0.25 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 1.0–1.3 cm. longis patentibus; antheris anguste oblongo-sagittatis paulo panduratis 0.45–0.5 cm. longis glabris paulo exsertis; ovario ovoideo ca. 0.2 cm. longo glabro; stigmate 0.15 cm. longo; nectariis compresse oblongo-ovoideis integris vel basi plus minusve connatis apice truncatis ovarium aequantibus vel paullulo superantibus; folliculis ignotis.

Stems relatively stout, minutely puberulent when young, glabrate and conspicuously lenticellate when fully mature; leaves broadly oval to broadly obovate-oval, apex obtuse or rounded, frequently very shortly mucronulate, base rounded, 9.5–17.5 cm. long, 4.5–10.0 cm. broad, firmly membranaceous, opaque, glabrous; petioles 0.6–1.6 cm. long, glabrous; stipular appendages intrapetiolar, numerous, dentiform-flagelliform; inflorescence corymbose or subumbelate, obscurely di- or trichotomous, bearing 8–20 yellow flowers; peduncle much shorter than the subtending leaves; pedicels 1.1–1.2 cm. long, somewhat accrescent after maturity, minutely appressed-puberulent; bracts narrowly elliptic-oblongeolate, 0.65–1.2 cm. long, more or less petalaceous, purplish, caducous; calyx-lobes oblong-elliptic, shortly acuminate, 0.9–1.1 cm. long, subcoriaceous, purplish, without minutely appressed puberulent, the internal squamellae dentiform-deltoid, very minutely erose; corolla salverform, minutely papillate without, the tube 1.5–1.7 cm.



long, about 0.35 cm. in diameter at the base, epistaminal appendages barely attaining the faucal annulus, about 0.25 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 1.0–1.3 cm. long, reflexed or spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers narrowly oblong-sagittate, slightly pandurate, 0.45–0.5 cm. long, glabrous, slightly exserted; ovary ovoid, about 0.2 cm. long, glabrous; stigma about 0.15 cm. long; nectaries compressed oblong-ovoid, separate or slightly connate at the base, apex truncate, about equalling or very slightly surpassing the ovary; follicles unknown.

EQUADOR: MANABI: in fruticetis siccis, El Recreo, Aug., 1893, *Eggers 15078* (M, TYPE, MBG, photograph and analytical drawings); GUAYAS: Toachi, alt. 400–860 m., Dec., 1883, *Sodiño 106/1* (B).

Distinguished from *P. trifida* by the peculiar, petalaceous bracts.

**28. *Prestonia robusta* Rusby, Descr. So. Am. Pl. 91. 1920.**

Stems relatively stout, glabrous and conspicuously lenticellate when fully mature; leaves broadly oval to obovate-oval, apex obtuse or rounded to very abruptly and shortly acuminate, base obtuse to rounded, 10–21 cm. long, 5.5–12.5 cm. broad, subcoriaceous, opaque, glabrous; petioles 1.4–1.6 cm. long, glabrous; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose or subumbellate, obscurely di- or trichotomously compound, bearing 10–20 greenish-white or yellowish flowers; peduncle much shorter than the subtending leaves, glabrous to very sparsely puberulent; pedicels 0.4–0.9 cm. long, somewhat accrescent after maturity, minutely puberulent-papillate; bracts oval to elliptic, 0.3–0.5 cm. long, somewhat foliaceous or tinted with purple, caducous; calyxlobes oval to broadly oblong-elliptic, acute to acuminate, 1.0–1.5 cm. long, coriaceous or subcoriaceous, somewhat suffused with purple, sparsely and minutely puberulent-papillate without, the internal squamellae dentiform-ligular, truncate or slightly erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.3–1.5 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages slightly exserted,

0.25–0.3 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers narrowly sagittate, 0.55 cm. long, glabrous or essentially so; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.12–0.15 cm. long; nectaries compressed-ovoid, separate or slightly connate at the base, about equalling the ovary; follicles unknown.

BOLIVIA: LA PAZ: Tumupasa, alt. 1800 ft., Dec. 15, 1901, *R. S. Williams 571* (NY, TYPE, MBG, photograph and analytical drawings); SANTA CRUZ: bosque, Buenavista, alt. 400 m., Dec. 30, 1925, *Steinbach 7376* (B); Montecito de Fuca, Buenavista, alt. 450 m., Sept. 29, 1916, *Steinbach 2863* (B).

**29. *Prestonia macroneura* (Muell.-Arg.) Woodson, comb. nov.**

*Haemadictyon macroneurum* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 169. 1860; Miers, Apoc. So. Am. 262. 1878.

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves broadly oval, apex obtuse to very shortly acuminate, base obtuse to rounded, 12–15 cm. long, 7–9 cm. broad, firmly membranaceous, opaque; petioles 0.5–0.8 cm. long; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence densely subumbellate-capitate, simple or very obscurely compound, bearing 15–20 congested, reddish flowers tinged with purple, yellow, and white; peduncle much shorter than the subtending leaves; pedicels 0.3–1.0 cm. long, somewhat accrescent after maturity; bracts oval to oblong-lanceolate, acute to acuminate, 0.4–1.0 cm. long, foliaceous, persistent; calyx-lobes oval to broadly elliptic, acuminate, 0.9–1.1 cm. long, green slightly tinged with purple at the base, the internal squamellae deltoid, minutely lacerate; corolla salverform, glabrous or very minutely papillate without, the tube 1.3–1.5 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages slightly exserted, about 0.4 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers sagittate, about 0.5 cm. long,

glabrous, slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.1–0.15 cm. long; nectaries compressed oblong-ovoid, separate or somewhat concrescent at the base, equalling or slightly surpassing the ovary; follicles unknown.

BRAZIL: AMAZONAS: in sepibus ad Porto dos Juris prope Cataract. Capatenses, Dec., year lacking, *Martius 3029* (M, TYPE, V, MBG, photograph and analytical drawings).

An examination of Vellozo's illustration of *Echites denticulata* (Icon. 3: pl. 30. 1830), a species with elongate inflorescence and inconspicuous bracts, does not appear to ally that plant with Martius' specimen, as indicated in Mueller's synonymy. The description of the color of the corolla has been adapted from Mueller.

30. *Prestonia trifida* (Poepp.) Woodson, in Gleason & A. C. Smith, Bull. Torrey Bot. Club 60: 392. 1933.

*Haemadictyon trifidum* Poepp. Nov. Gen. 3: 67. pl. 275. 1845; Miers, Apoc. So. Am. 261. 1878.

*Prestonia (Haemadictyon) Evansii* S. Moore, Trans. Linn. Soc. Bot. II. 4: 395. 1895.

*Prestonia glabrata* K. Sch. Verhandl. Bot. Ver. Brandenburg 47: 189. 1905, not HBK.

Stems relatively stout, inconspicuously puberulent when very young, soon becoming glabrate and conspicuously lenticellate; leaves broadly ovate to broadly oval, apex very abruptly and shortly acuminate to obtuse, base broadly obtuse-rounded, 9–31 cm. long, 4.5–14.5 cm. broad, coriaceous or subcoriaceous, opaque or slightly nitidulous above, somewhat glaucescent beneath, glabrous; petioles 0.8–2.5 cm. long, glabrous; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose, tri- or rarely dichotomous, bearing 15–30 yellow flowers; peduncle much shorter than the subtending leaves, very minutely puberulent to glabrate; pedicels 0.6–1.8 cm. long, very minutely puberulent-papillate to glabrate, somewhat accrescent after maturity; bracts very minute, broadly ovate-dentiform to ovate-lanceolate, scarious, persistent; calyxlobes oblong-elliptic, acute to very shortly acuminate, 0.9–1.5 cm. long, coriaceous, minutely appressed-puberulent to pu-

berulent-papillate, more or less strongly suffused with purple, the internal squamellae deltoid, minutely erose or lacerate; corolla salverform, glabrous to minutely puberulent-papillate without, the tube 1.5–1.8 cm. long, about 0.35 cm. in diameter at the base, epistaminal appendages slightly exserted, 0.2–0.4 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers oblong-sagittate, slightly pandurate, 0.5–0.6 cm. long, glabrous, slightly exserted; ovary ovoid, about 0.125 cm. long, glabrous, stigma 0.1–0.15 cm. long; nectaries compressed ovoid, separate or more or less connate at the base, about equalling the ovary; follicles unknown.

COLOMBIA: CHOCO: between La Oveja and Quibdo, April 1–2, 1931, *Archer 1749* (US).

PERU: LORETO: forest, Mishuyacu, near Iquitos, alt. 100 m., Jan., 1930, *Klug 774* (FM, US); same locality, Febr.–March, 1930, *Klug 915* (FM, US); Tarapoto, Dec., 1902, *Ute 6604* (B, DL); silva non inundata, Rio Huallaga, Yurimaguas, Febr. 11, 1924, *Kuhlmann 21851* (B); Tarapoto, alt. 150 m., Dec., 1929, *L. Williams 6049* (FM); Maynas, silvae primaevae, Febr., 1831, *Poeppig 2161* (V, TYPE, MBG, photograph and analytical drawings).

BRAZIL: MATTO GROSSO: ad ripas fl. Paraguay inter Santa Cruz et Villa Maria, Dec., 1891, *Moore 819* (B, NY, MBG, photograph and analytical drawings); near source of the Jatuarana River, Machado River region, *Krukoff 1545* (NY).

### 31. *Prestonia vana* Woodson, spec. nov.

Fruticosa volubilis ut creditur; ramulis gracilibus maturitate glabris conspicue lenticellatis; foliis late ovalibus apice rotundatis breviter acuminato-mucronatis basi late obtusis rotundatisve 13–16 cm. longis 8.0–9.5 cm. latis coriaceis subcoriaceisve glaberrimis opacis superne paulo lucentibus; petiolis 1.0–1.2 cm. longis glabris; appendicibus stipulaceis intrapetiolaribus pectinatis numerosis; inflorescentiis corymbosis flores 20–25 speciosos viridi-lutescentes rubicundos gerentibus; pedunculi dichotomi foliis bis terve brevioris partibus florigeris minute denseque puberulis sterilibus glabris; pedicellis 1.7–2.0 cm. longis minute denseque puberulis; bracteis ovato-lanceolatis 0.2–0.3 cm. longis scariaceis haud caducis; calycis laciniis oblongo-ellipticis apice acute acuminatis 1.2–1.3 cm. longis subcoriaceis viridibus vel paulo purpurissatis extus minute

sparseque puberulis intus glabris squamellis profunde irregulariterque laceratis; corollae salverformis tubo 1.5–1.6 cm. longo basi ca. 0.25 cm. diametro metiente extus minute velutino intus prope insertionem staminum molliter puberulo caeterumque glabro appendicibus epistaminalibus linearibus ca. 0.4–0.45 cm. longis valde exsertis annulo faucium conspicue incrassato lobis oblique obovato-dolabriformibus conspicue acuminatis 0.7–0.8 cm. longis patentibus; antheris oblongo-sagittatis 0.5 cm. longis dorso minute denseque puberulis apice exsertis; ovario ovoideo ca. 0.125 cm. longo sparse minuteque pilosulo; stigmatibus subcapitato-maniculato ca. 0.15 cm. longo; nectariis incrassatis compresse ovoideis ovarium paulo superantibus; folliculis ignotis.

Stems somewhat slender, glabrous, conspicuously lenticellate at maturity; leaves broadly oval, apex rounded, usually acuminate-mucronate, base broadly obtuse to rounded, 13–16 cm. long, 8.0–9.5 cm. broad, coriaceous to subcoriaceous, glabrous, opaque, or the upper surface somewhat shining; petioles 1.0–1.2 cm. long, glabrous; stipular appendages intrapetiolar, pectinate, numerous; inflorescence corymbose, bearing 20–25 showy, greenish-yellow, red-flushed flowers; peduncle twice to thrice shorter than the subtending leaves, the floriferous branches minutely and densely puberulent, the sterile axis glabrous; pedicels 1.7–2.0 cm. long, minutely and densely puberulent; bracts ovate-lanceolate, 0.2–0.3 cm. long, scarious or very slightly foliaceous when very young, persistent; calyxlobes oblong-elliptic, apex acutely acuminate, 1.2–1.3 cm. long, subcoriaceous, green or very slightly suffused with purple, without minutely and rather sparsely puberulous, within glabrous, the squamellae deeply and irregularly lacerate; corollatube 1.5–1.6 cm. long, about 0.25 cm. in diameter at the base, minutely velutinous without, softly puberulent within about the insertion of the stamens, epistaminal appendages linear, 0.4–0.45 cm. long, conspicuously exserted, faucal annulus conspicuously thickened, the lobes obliquely obovate-dolabriform, conspicuously acuminate, 0.7–0.8 cm. long, reflexed; anthers oblong-sagittate, 0.5 cm. long, minutely and densely puberulent

dorsally, the tips slightly exserted; ovary ovoid, about 0.125 cm. long, sparsely and minutely pilosulose; stigma subcapitate-maniculate, about 0.15 cm. long; nectaries fleshy, essentially separate, compressed-ovoid, slightly surpassing the ovary; follicles unknown.

PERU: LORETO: Balsapuerto, alt. about 220 m., forest, May, 1933, *Klug 3066* (MBG, TYPE).

This species is quite likely to be mistaken for *P. trifida* upon first sight. From that species, however, it differs in the looser inflorescence, longer pedicels, more delicate texture of the calyx-lobes, and more conspicuously exserted epistaminal appendages, in addition to the pubescent flowers and anthers as indicated in the key to species.

**32. *Prestonia plumierifolia* Mgf. Notizblatt 10: 1038. 1930.**

Stems relatively stout, minutely appressed-puberulent when young, glabrate and conspicuously lenticellate when fully mature; leaves obovate to obovate-lanceolate, apex obtuse or rounded, infrequently extremely abruptly and shortly acuminate to submucronate, base obtuse, cuneate, 8–16 cm. long, 3–6 cm. broad, subcoriaceous, opaque, or the upper surface slightly nitidulous, sparsely and minutely puberulent when very young, soon perfectly glabrate; petioles 0.5–1.5 cm. long, minutely and rather sparsely puberulent-papillate to glabrate; stipular appendages intrapetiolar, numerous, minutely and narrowly dentiform; inflorescence corymbose, dichotomous, bearing 8–30 greenish-yellow flowers; peduncle somewhat shorter than the subtending leaves; pedicels 0.4–1.0 cm. long, somewhat accrescent after maturity, minutely ferruginous-puberulent; bracts ovate-lanceolate, 0.1 cm. long or less, scarious; calyx-lobes oblong-elliptic, acute to acuminate, 0.6–0.8 cm. long, subcoriaceous, minutely and sparsely puberulent-papillate to glabrate, conspicuously suffused with purple, the internal squamellae deltoid-dentiform, minutely erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.2–1.5 cm. long, about 0.35 cm. in diameter at the base, epistaminal appendages barely exserted, 0.3 cm. long, faucal annulus conspicuously

thickened, the lobes obliquely obovate, shortly acuminate, 0.7–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exerted, narrowly sagittate, slightly pandurate, 0.5 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.1–0.15 cm. long; nectaries compressed-ovoid, concrescent at the base, somewhat shorter than the ovary; follicles unknown.

BRAZIL: in hortum paraënsem, introductu (prov. Rio Purus), Aug. 9, 1905, *Huber 7030* (B, ISOTYPE, MBG, photograph and analytical drawings).

This species is founded upon a cultivated specimen said to have been introduced from the region of the Rio Purus, State of Amazonas, Brazil.

**33. *Prestonia amazonica* (Benth.) Macbr.** Field Mus. Publ. Bot. 11: 34. 1931.

*Haemadictyon Amazonicum* Benth. ex Muell.-Arg. in Mart.

Fl. Bras. 6<sup>1</sup>: 166. 1860; Miers, Apoc. So. Am. 262. 1878.

Stems relatively stout, minutely puberulent when young, becoming glabrate and conspicuously lenticellate when fully mature; leaves broadly oval, apex abruptly and shortly acuminate, base obtuse or rounded, 7–13 cm. long, 3–7 cm. broad, firmly membranaceous, opaque, minutely puberulent when young, glabrate when mature; petioles 0.8–1.1 cm. long, minutely puberulent to glabrate; stipular appendages intrapetiolar, numerous, minutely denticulate; inflorescence corymbose or subumbellate, simple or obscurely dichotomous, bearing 6–15 greenish-yellow flowers; peduncle somewhat shorter than the subtending leaves, minutely and sparsely puberulent to glabrate; pedicels 1.5–1.7 cm. long, somewhat accrescent after maturity, minutely puberulent-papillate; bracts minutely ovate-lanceolate, 0.1–0.3 cm. long, scarious; calyx-lobes ovate, acuminate, 0.5–0.6 cm. long, subcoriaceous, suffused with purple, minutely papillate without, the internal squamellae very deeply lacerate; corolla salverform, densely papillate without, the tube 1.3–1.4 cm. long, about 0.25 cm. in diameter at the base, epistaminal appendages exerted, 0.4 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate,

0.7–0.8 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, 0.45–0.5 cm. long, glabrous; ovary ovoid, about 0.1 cm. long, minutely papillate; stigma 0.125 cm. long; nectaries compressed-obovoid, concrescent at the base, about equalling the ovary; follicles unknown.

BRAZIL: PARA: ad ripas fl. Trombetas et lacus Quiriquiry, Dec., 1849, *Spruce 239* (M, TYPE, V, MBG, photograph and analytical drawings).

**34. *Prestonia Lindleyana*** Woodson, in Gleason & A. C. Smith, *Bull. Torrey Bot. Club* 60: 392. 1933.

*Haemadictyon calycinum* Lindl. ex Miers, *Apoc. So. Am.* 259. 1878, not Muell.-Arg.

Stems glabrous, relatively slender, not evidently lenticellate; leaves oblong- to obovate-elliptic, apex shortly acuminate, base obtuse to rounded, 10–16 cm. long, 3–7 cm. broad, firmly membranaceous to subcoriaceous, glabrous, pale green above, somewhat glaucescent beneath; petioles 0.3–0.8 cm. long, glabrous; stipular appendages numerous, interpetiolar, minutely and narrowly dentiform-flagelliform; inflorescence densely racemose, simple, bearing 10–20 yellowish flowers; peduncle somewhat shorter than the subtending leaves; pedicels 0.5–1.0 cm. long, minutely appressed-puberulent; bracts ovate or ovate-lanceolate, 0.1–0.2 cm. long, slightly foliaceous; calyx-lobes ovate to ovate-oblong, acute to acuminate, 0.9–1.0 cm. long, membranaceous, green, flushed with purple at the base, glabrous, the internal squamellae broadly deltoid-trigonal, entire or slightly erose-undulate; corolla salverform, glabrous or very minutely papillate without, the tube 0.9–1.5 cm. long, about 0.25 cm. in diameter at the base, epistaminal appendages exserted, 0.25 cm. long, faecal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.6–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, slightly pandurate, 0.4–0.45 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, densely and minutely papillate; stigma 0.125–0.15 cm. long; nectaries com-



pressed obovoid, separate or slightly conerescent, equalling or slightly surpassing the ovary; follicles unknown.

BRAZIL: AMAZONAS: prope Barra, Prov. Rio Negro, Oct., 1851, *Spruce 1882* (B, Bx, Camb., TYPE, V, MBG, photograph and analytical drawings); Municipality Humayta, near Livramento, on Rio Livramento, on varzea land, Oct. 12–Nov. 6, 1934, *Krukoff 6763* (NY); MATTO GROSSO: on varzea land near river-shore, near Tabajaa, upper Machado River region, Nov.–Dec., 1931, *Krukoff 1427* (MBG, NY).

**35. *Prestonia denticulata* (Vell.) Woodson, comb. nov.**

*Echites denticulata* Vell. Fl. Flum. 110. 1830; Icon. 3: *pl.* 30. 1827; A. DC. in DC. Prodr. 8: 455. 1844.

*Echites suberosa* Vell. Fl. Flum. 111. 1830; Icon. 3: *pl.* 34. 1827; A. DC. loc. cit. 475. 1844.

*Haemadictyon Gaudichaudii* A. DC. loc. cit. 426. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 168. 1860; Miers, Apoc. So. Am. 256. 1878.

*Haemadictyon denticulatum* (Vell.) Miers, loc. cit. 257. 1878.

*Haemadictyon ovatum* Miers, loc. cit. 258. 1878.

*Prestonia Gaudichaudii* (A. DC.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895.

Stems relatively slender, minutely appressed-puberulent when very young, becoming glabrate and rather inconspicuously lenticellate when fully mature; leaves oblong-elliptic to broadly oval, apex obtuse to shortly acuminate, base obtuse or rounded, 6–13 cm. long, 3–6 cm. broad, firmly membranaceous, opaque, puberulent when young, above glabrous, beneath minutely and rather sparsely papillate when fully mature; petioles 0.2–1.1 cm. long, minutely appressed-puberulent to glabrate; stipular appendages intrapetiolar, numerous, narrowly dentiform; inflorescence racemose, simple, bearing 12–30 yellow flowers; peduncle about equalling or somewhat shorter than the subtending leaves, sparsely appressed-puberulent to glabrate; pedicels 0.4–1.2 cm. long, densely and minutely puberulent; bracts minutely ovate-lanceolate, 0.1–0.3 cm. long, scarious; calyx-lobes broadly oblong- to ovate-elliptic, acute to shortly acuminate, 0.4–0.65 cm. long, subcoriaceous to rigidly membranaceous, more or less suffused with purple, minutely puberulent to puberulent-papillate, the internal squamellae

deltoid-ligular, entire or very minutely erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.1–1.3 cm. long, about 0.25–0.3 cm. in diameter at the base, epistaminal appendages somewhat exserted, 0.25–0.32 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.45–0.65 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, sagittate, 0.4–0.55 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.1–0.125 cm. long; nectaries compressed-ovoid, irregularly conrescent at the base, equalling or slightly surpassing the ovary; follicles relatively long and slender, conspicuously moniliform, 20–39 cm. long, glabrous or very sparsely and minutely puberulent-papillate; seeds 1.2–1.3 cm. long, the pale yellowish coma 1.5–1.9 cm. long.

BRAZIL: RIO DE JANEIRO: in collibus umbrosis inter frutices, vic. Rio de Janeiro, 1835, *Gaudichaud* 533 (B, DC, DL, MBG, photograph and analytical drawings); Rio de Janeiro, date lacking, *Glaziov* 12954 (B); same data, *Glaziov* 3728 (Bx); same data, 1872, *Glaziov* 4881 (B); Barra do Pirahy, April 13, 1926, *Hoehne & Gehrt* 17319 (B); Morro de São João, Jan. 8, 1887, *Schenck* 1947 (B); Serra da Bica, Febr., 1897, *Ule* 4285 (B); in silvis prope Hortum Botanicum Rio de Janeiro, Febr. 13, 1916, *Constantino* 7787 (B); DATA INCOMPLETE: *Sellow* s.n. (B); *Riedel* s.n. (B, BB, G, U, V); *Regel* s.n. (Camb.); *Forrest* s.n. (Camb.).

*P. denticulata* is one of the most uniform and distinctive species of the genus. Consequently Vellozo's epithets may be rather safely interpreted as pertaining to this species, particularly since they refer to plants of Rio de Janeiro, where *P. denticulata* is apparently frequent and endemic.

36. *Prestonia Meg'agros* (Vell.) Woodson, Ann. Mo. Bot. Gard. 21: 623. 1934.

*Echites Meg'agros* Vell. Fl. Flum. 110. 1830; Icon. 3: pl. 33. 1827.

*Haemadictyon asperum* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 169. 1860; Miers, Apoc. So. Am. 258. 1878.

*Haemadictyon megalagrion* Muell.-Arg. loc. cit. 170. 1860.

*Prestonia megalagrion* (Muell.-Arg.) Miers, loc. cit. 149. 1878.

? *Prestonia laeta* Miers, loc. cit. 1878.

Stems relatively stout, densely ferruginous-hirtellous to glabrate; leaves broadly oval to broadly obovate, apex obtuse or rounded, occasionally very shortly and abruptly acuminate-submucronate, 11–20 cm. long, 5–12 cm. broad, coriaceous or subcoriaceous, beneath opaque, densely ferruginous-puberulent to subtomentulose, above somewhat nitidulous, ferruginous-puberulent to glabrate; petioles 1.0–1.4 cm. long, ferruginous-hirtellous; stipular appendages intrapetiolar, numerous, minutely dentiform; inflorescence corymbose, di- or trichotomous, bearing 20–40 yellowish flowers; peduncle somewhat shorter than the subtending leaves, ferruginous-hirtellous; pedicels 0.6–1.2 cm. long, somewhat accrescent after maturity, minutely ferruginous-hirtellous; bracts narrowly lanceolate, 0.4–0.7 cm. long, scarious or somewhat petalaceous; calyx-lobes oblong-lanceolate, acuminate, 1.0–1.6 cm. long, minutely ferruginous-hirtellous without, subcoriaceous, deeply suffused with purple, the internal squamellae broadly deltoid, minutely emarginate or erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.3–1.4 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages slightly exserted, 0.3–0.35 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 1.0–1.2 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, slightly pandurate, 0.55 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, minutely papillate; stigma 0.15 cm. long; nectaries compressed-ovoid, more or less conerescent at the base, slightly shorter than the ovary; follicles unknown.

BRAZIL: PARA: Obidos, silva non inundata, July 23, 1927, *Ducke 21602* (B, S); Obidos, silva secundaria, May 11, 1905, *Ducke 21634* (B).

These specimens compare very well with Vellozo's illustration, particularly with regard to the peculiar indument.

**37. *Prestonia obovata*** Standl. Jour. Wash. Acad. Sci. 15: 459. 1925.

Stems relatively stout, glabrous, conspicuously lenticellate when fully mature; leaves obovate to obovate-oblong, apex ob-

tuse or rounded, occasionally abruptly and very shortly acuminate-submucronate, base obtuse, somewhat cuneate, 9–16 cm. long, 4–8 cm. broad, coriaceous or subcoriaceous, glabrous, above dark green and somewhat nitidulous, beneath paler and somewhat glaucescent; petioles 0.7–1.2 cm. long, glabrous, or very sparsely and minutely pilosulose; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose, dichotomous, bearing 10–30 purplish-yellow flowers; peduncle much shorter than the subtending leaves, glabrous; pedicels 1.1–1.5 cm. long, minutely and sparsely pilosulose to glabrate; bracts minutely ovate-lanceolate, 0.15–0.2 cm. long, scarious; calyx-lobes oblong-elliptic, acuminate, 1.0–1.2 cm. long, coriaceous, minutely papillate to glabrate without, purplish, the internal squamellae deltoid-dentiform, minutely erose; corolla salverform, minutely papillate without, 1.0–1.3 cm. long, about 0.35 cm. in diameter at the base, epistaminal appendages wholly included, 0.12–0.15 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers narrowly sagittate, slightly pandurate, 0.5–0.55 cm. long, glabrous, slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries concrescent, rather thick and fleshy, entire or slightly undulate, somewhat surpassing the ovary; follicles unknown.

PANAMA: CANAL ZONE: trail between Gamboa and Cruces, July 2, 1911, *Pittier 3767* (G, US, TYPE, MBG, photograph and analytical drawings); Barbour-Lathrop Trail, Barro Colorado Island, Oct. 12, 1931, *Shattuck 129* (MBG).

**38. *Prestonia concolor* (S. F. Blake) Woodson**, in Standl. & Record, Field Mus. Publ. Bot. **12**: 327. 1936.

*Belandra concolor* S. F. Blake, Contr. Gray Herb. **52**: 78. 1917.

Stems relatively slender, minutely and rather sparsely pilosulose when very young, glabrate and rather inconspicuously lenticellate when fully mature; leaves oblong-elliptic, apex shortly acuminate, base obtuse to rounded, 9–13 cm. long, 3–5 cm. broad, subcoriaceous, glabrous, pale green, above slightly

nitidulous, beneath opaque; petioles 0.6–0.9 cm. long, glabrous to minutely papillate; stipular appendages interpetiolar, numerous, very minutely dentiform-flagelliform; inflorescence racemose, simple, bearing 30–40 greenish-yellow (?) flowers; peduncle about equalling the subtending leaves, glabrous or minutely papillate; pedicels 0.7–1.0 cm. long, somewhat accrescent after maturity, minutely papillate; bracts linear-lanceolate, 0.05–0.07 cm. long, scarious; calyx-lobes ovate-elliptic, acute to acuminate, 0.4–0.5 cm. long, membranaceous or slightly subcoriaceous, deeply suffused with purple, minutely papillate without, the internal squamellae deltoid, minutely erose or lacerate; corolla salverform, glabrous or very minutely papillate without, the tube 1.5–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages wholly included, 0.17–0.2 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.8–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, narrowly oblong-sagittate, 0.48–0.5 cm. long, glabrous or very minutely puberulent-papillate; ovary ovoid, about 0.125 cm. long, glabrous; stigma 0.1 cm. long; nectaries concrescent, entire or slightly undulate, somewhat surpassing the ovary; follicles unknown.

BRITISH HONDURAS: low banks of Rio Grande, March 25, 1907, *Peck 953* (G, TYPE, MBG, photograph and analytical drawings).

**39. *Prestonia versicolor* Woodson, spec. nov.**

Suffruticosa volubilis omnino glabra; ramulis crassiusculis maturitate conspicue lenticellatis; foliis ovalibus oblongo-ellipticisve apice abrupte breviterque acuminatis basi obtusis vel rotundatis 10–17 cm. longis 5–9 cm. latis rigide membranaceis opacis; petiolis 1.3–2.1 cm. longis; appendicibus stipulaceis interpetiolaribus multis minutissime denticularibus; inflorescentiis subcorymbosis dichotome divisis; pedunculo foliis multo brevior; pedicellis 1.4–1.6 cm. longis post maturitatem paulo accrescentibus glabris vel minutissime papillatis; bracteis minutissimis; calycis laciniis oblongo-ellipticis acutis acuminatisve 0.8–1.0 cm. longis membranaceis viridibus incon-

spicue purpurissatis squamellis denticulato-trigonalibus integris; corollae salverformis tubo 1.2–1.6 cm. longo basi ca. 0.3 cm. diametro metiente prope fauces paulo angustato appendicibus epistaminalibus omnino inclusis 0.15 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.7–0.9 cm. longis patentibus; antheris paulo exsertis oblongo-sagittatis paululo panduratis 0.6 cm. longis glabris; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus 0.15 cm. longo; nectariis concrecentibus margine leviter erosis tenuibus haud incrassatis ovarium conspicue superantibus; folliculis ignotis.

Plants completely glabrous; stems relatively stout, conspicuously lenticellate when fully mature; leaves oval or oblong-elliptic, apex abruptly and shortly acuminate, base obtuse or rounded, 10–17 cm. long, 5–9 cm. broad, firmly membranaceous, opaque, petioles 1.3–2.1 cm. long; stipular appendages interpetiolar, numerous, very minutely dentiform; inflorescence subcorymbose, dichotomous; peduncle much shorter than the subtending leaves; pedicels 1.4–1.6 cm. long, somewhat accrescent after maturity, glabrous or very minutely papillate; bracts very minute, scarcely visible; calyx-lobes oblong-elliptic, acute to acuminate, 0.8–1.0 cm. long, membranaceous, green inconspicuously flushed with purple, the internal squamellae dentiform-trigonal, entire; corolla salverform, glabrous without, the tube 1.2–1.6 cm. long, about 0.3 cm. in diameter at the base, slightly constricting toward the orifice, epistaminal appendages wholly included, 0.15 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, slightly pandurate, 0.6 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries completely concrecent, thin and more or less diaphanous, not fleshy, slightly erose, conspicuously surpassing the ovary; follicles unknown.

PANAMA: COLON: Cana and vicinity, alt. 2000–6500 ft., April 17–June 8, 1908, E. S. Williams 940 (NY, TYPE, MBG, photograph and analytical drawings); Perme, April 23, 1933, Cooper 237 (NY).

The color of the flowers is reported by Williams as "Tube pink, divisions greenish outside, purple lines within."

**40. *Prestonia peregrina* Woodson, spec. nov.**

Suffruticosa volubilis; ramulis crassiusculis juventate minute appresse-puberulis maturitate minute irregulariterque scabridulis conspicue lenticellatis; foliis oblongo-ellipticis apice abrupte breviterque acuminatis basi obtusis 8–17 cm. longis 3–7 cm. latis rigide membranaceis opacis omnino glabris; petiolis 0.9–2.0 cm. longis minute sparseque puberulo-papillatis; appendicibus stipulaceis interpetiolaribus multis minute denticulo-flagelliformibus; inflorescentiis subcorymbosis dichotome subdivisis flores 30–60 albo-luteos gerentibus; pedunculo folia superante glabro vel indistincte irregulariterque puberulo-papillato; pedicellis 0.7–1.5 cm. longis post maturitatemve paulo accrescentibus minute papillatis; bracteis ovato-lanceolatis 0.1–0.15 cm. longis scariaceis; calycis laciniis oblongo-ellipticis acuminatis 1.1–1.5 cm. longis subcoriaceis saturate purpurissatis extus glabris squamellis deltoideis minute erosis; corollae salverformis extus glabrae vel minutissime papillatae tubo 1.6–1.8 cm. longo basi ca. 0.3 cm. diametro metiente appendicibus epistaminalibus omnino inclusis ca. 0.1 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.7–0.9 cm. longis patentibus; antheris paulo exsertis oblongo-sagittatis paululo panduratis 0.5–0.6 cm. longis glabris vel minutissime papillatis; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus 0.125–0.15 cm. longo; nectariis conerescentibus tenuibus haud incrassatis margine minute erosis ovarium conspicue superantibus; folliculis gracilimimis continuis leviter falcatis apice saepius connatis 36–38 cm. longis glabris; seminibus ignotis.

Stems relatively stout, minutely appressed-puberulent when young, minutely and irregularly scabridulous and conspicuously lenticellate when fully mature; leaves oblong-elliptic, apex abruptly and shortly acuminate, base obtuse, 8–17 cm. long, 3–7 cm. broad, firmly membranaceous, opaque, glabrous; petioles 0.9–2.0 cm. long, minutely and sparsely puberulent-papillate; stipular appendages interpetiolar, numerous, mi-

nutely dentiform-flagelliform; inflorescence subcorymbose, dichotomously subdivided, bearing 30–60 yellowish flowers; peduncle somewhat surpassing the subtending leaves, glabrous or indistinctly and irregularly puberulent-papillate; pedicels 0.7–1.5 cm. long, or somewhat accrescent after maturity, minutely papillate; bracts ovate-lanceolate, 0.1–0.15 cm. long, scariaceous; calyx-lobes oblong-elliptic, acuminate, 1.1–1.5 cm. long, subcoriaceous, deeply suffused with purple, glabrous, the internal squamellae deltoid, minutely erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.6–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages wholly included, about 0.1 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.7–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, slightly pandurate, 0.5–0.6 cm. long, glabrous or very minutely papillate; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.125–0.15 cm. long; nectaries wholly concrescent, thin and somewhat diaphanous, not fleshy, minutely erose, conspicuously surpassing the ovary; follicles relatively slender, continuous, somewhat falcate, the tips frequently connate, 36–38 cm. long, glabrous; seeds unknown.

ECUADOR: GUAYAS: Balao, March, 1892, *Eggers 14527* (M); FIOFINCHA: Tandapi, ad marg. silvulae, July, 1920, *Heilborn 771* (DL, G, S, TYPE, MBG, photograph and analytical drawings).

The affinities of this species accentuate still further the intimate relationship of certain elements of the flora of Ecuador for the flora of Central America.

#### 41. *Prestonia vallis* Woodson, spec. nov.

Fruticosa vel suffruticosa volubilis; ramulis gracilibus glaberrimis maturitate conspicue lenticellatis; foliis ovalibus apice breviter acuminatis basi late obtusis 10–14 cm. longis 4.5–6.5 cm. latis membranaceis glaberrimis utrinque opacis; petiolis 0.6–0.8 cm. longis glabris; appendicibus stipulaceis intrapetiolaribus minute pectinatis numerosis; inflorescentiis corymbosis dichotomis flores 20–25 speciosos brunneos gerenti-



bus; pedunculo petiolos bis terve superante minutissime puberulo haud ferrugineo; pedicellis 1.0–1.2 cm. longis minutissime puberulo-papillatis; bracteis ovato-lanceolatis 0.15–0.25 cm. longis scariaceis; calycis laciniis ovato-lanceolatis acute acuminatis 1.3–1.4 cm. longis firmiter membranaceis foliaceis vel paululo purpurissatis glaberrimis squamellis deltoideis minute irregulariterque erosis; corollae salverformis tubo 1.4–1.5 cm. longo basi ca. 0.18–0.2 cm. diametro metiente extus glabro intus prope insertionem staminum molliter puberulo appendicibus epistaminalibus oblongis 0.1–0.125 cm. longis profunde inclusis annulo faucium conspicue incrassato lobis oblique obovatis 1.5–1.7 cm. longis patentibus; antheris lanceolato-sagittatis 0.6 cm. longis dorso minute puberulis apice paulo exsertis; ovario ovoideo 0.1 cm. longo apice inconspicuissime barbellato; stigmatibus subcapitato-maniculato ca. 0.15 cm. longo; nectariis basi concrescentibus ubique paululo incrassatis caeterumque delicate membranaceis plus minusve foliaceis minute pilosulis ovarium ca. dimidio superantibus; folliculis ignotis.

Stems relatively slender, glabrous, conspicuously lenticellate when fully mature; leaves oval, apex shortly acuminate, base broadly obtuse, 10–14 cm. long, 4.5–6.5 cm. broad, membranaceous, glabrous, opaque throughout; petioles 0.6–0.8 cm. long, glabrous; stipular appendages intrapetiolar, minutely pectinate, numerous; inflorescence corymbose, dichotomous, bearing 20–25 showy brownish flowers; peduncle about twice to thrice surpassing the subtending petioles, minutely, but not ferruginously, puberulent; pedicels 1.0–1.2 cm. long, minutely puberulent-papillate; bracts ovate-lanceolate, 0.15–0.25 cm. long, scarious; calyx-lobes ovate-lanceolate, acutely acuminate, 1.3–1.4 cm. long, firmly membranaceous, foliaceous or very slightly suffused with purple, glabrous, the squamellae deltoid, minutely and irregularly erose; corolla salverform, the tube 1.4–1.5 cm. long, about 0.18–0.2 cm. in diameter at the base, glabrous without, softly pubescent within near the insertion of the stamens, epistaminal appendages oblong, 0.1–0.125 cm. long, deeply included, faucal annulus conspicuously thickened, the lobes obliquely obovate, 1.5–1.7 cm. long, reflexed;

anthers lanceolate-sagittate, 0.6 cm. long, minutely puberulent dorsally, the tips slightly exserted; ovary ovoid, about 0.1 cm. long, the tips very inconspicuously barbellate, otherwise glabrous; stigma subcapitate-maniculate, about 0.15 cm. long; nectaries somewhat surpassing the ovary, conerescent and somewhat incrassate at the base, otherwise membranaceous and more or less foliaceous, entire or essentially so save for the five component divisions, minutely and sparsely pilosulose; follicles unknown.

COLOMBIA: VALLE DEL CAUCA: Urwald, Candelaria, alt. 2200 m., Jan. 1, 1931, *Dryander 1042* (B, TYPE, MBG, photograph and analytical drawings).

The foliaceous, puberulent nectary is the striking feature of this species, the membranaceous texture of which allies it to the species of § *Annulares* indigenous to Central America.

**42. *Prestonia Schippii* Woodson, spec. nov.**

Suffruticosa volubilis; ramulis gracilibus juventate minute puberulo-papillatis mox glabratis maturitate conspicue sed minute lenticellatis; foliis oblongo-ellipticis apice abrupte breviterque acuminatis basi obtusis rotundatisve 10–17 cm. longis 4–7 cm. latis rigidiuscule membranaceis opacis glabris; petiolis 1.2–1.6 cm. longis glabris rariusve minutissime papillatis; appendicibus stipulaceis intrapetiolaribus multis minutissime denticulato-flagelliformibus; inflorescentiis subcorymbosis simplicibus flores 10–12 gilvos gerentibus; pedunculo foliis multo brevior glabro; pedicellis 1.2–1.5 cm. longis post maturitatem paulo accrescentibus glabris vel minutissime papillatis; bracteis ovato-lanceolatis 0.1–0.2 cm. longis scariaceis vel rarius majoribus subfoliaceis; calycis laciniis obovato-ellipticis acutis 1.0–1.2 cm. longis glabris subcoriaceis paululo purpurissatis squamellis denticulato-trigonalibus integris; corollae salverformis extus minute papillatae tubo 1.3–1.4 cm. longo basi ca. 0.3 cm. diametro metiente appendicibus epistaminalibus omnino inclusis ca. 0.3 cm. longis annulo faucium conspicue incrassato lobis oblique obovatis breviter acuminatis 0.9–1.0 cm. longis patentibus; antheris paulo exsertis oblongo-sagittatis 0.5 cm. longis dorso minute hirtellis; ovario ovoideo

ca. 0.15 cm. longo glabro; stigmatē 0.125 cm. longo; nectariis conerescentibus tenuibus haud incrassatis margine erosis ovarium conspicue superantibus; folliculis ignotis.

Stems relatively slender, minutely puberulent-papillate when young, soon becoming glabrate and conspicuously but minutely lenticellate when fully mature; leaves oblong-elliptic, apex abruptly and shortly acuminate, base obtuse or rounded, 10–17 cm. long, 4–7 cm. broad, firmly membranaceous, opaque, glabrous; petioles 1.2–1.6 cm. long, glabrous or minutely papillate; stipular appendages intrapetiolar, numerous, very minutely dentiform-flagelliform; inflorescence subcorymbose, simple, bearing 10–12 cream-colored flowers; peduncle much shorter than the subtending leaves, glabrous; pedicels 1.2–1.5 cm. long, somewhat accrescent after maturity, glabrous or very minutely papillate; bracts ovate-lanceolate, 0.1–0.2 cm. long, scariaceous, or rarely the lowermost somewhat larger and subfoliaceous; calyx-lobes narrowly obovate-elliptic, acute, 1.0–1.2 cm. long, glabrous, subcoriaceous, slightly purple-tinted, the internal squamellae denticulate-trigonal, entire; corolla salverform, minutely papillate without, the tube 1.3–1.4 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages wholly included, about 0.3 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.9–1.0 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers oblong-sagittate, slightly pandurate, 0.5 cm. long, dorsally minutely hirtellous, slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.125 cm. long; nectaries wholly conerescent, thin and somewhat diaphanous, not fleshy, slightly erose, conspicuously surpassing the ovary; follicles unknown.

BRITISH HONDURAS: rare, climbing over low trees in forest, Eldorado, alt. 200 ft., Sept. 22, year lacking, *Schipp S-328* (FM, TYPE, MBG, photograph and analytical drawings).

The affinities of this species are outlined in the key to species. It is the second species of § *Annulares* to be reported from British Honduras, apparently the northernmost range of the section.

**43. *Prestonia guatemalensis* Woodson, spec. nov.**

Fruticosa volubilis; ramulis sat crassiusculis teretibus glabris maturitate conspicue lenticellato-verrucosis; foliis breviter petiolatis late obovato-ellipticis apice breviter acuteque acuminatis basi obtuse cuneatis 18–25 cm. longis 8–10 cm. latis firme membranaceis glaberrimis; petiolis 1.0–1.5 cm. longis; appendicibus stipulaceis interpetiolaribus anguste dentiformibus multis; inflorescentiis lateralibus bis terve dichotome divisis plurifloris; pedunculo post maturitatem 5.5–6.0 cm. longo glabro lenticellato-verrucoso; pedicellis 0.9–1.2 cm. longis minute papillatis (?); calycis laciniis latiuscule ellipticis obtusiusculis vel late acutis 0.7–0.9 cm. longis subcoriaceis dilute viridibus ut creditur hand purpurissatis extus intusque minute papillatis squamellis sat parvis acuminatis; corollae salverformis ut creditur luteae tubo 1.8–2.0 cm. longo basi ca. 0.2–0.225 cm. diametro metiente extus glabro intus prope insertionem staminum minute puberulo caeterumque glabriusculo appendicibus linearibus integris valde exsertis faucibus conspicue calloso-incrassatis lobis oblique obovatis minute acuminatis 1.2–1.3 cm. longis extus minutissime papillatis intus glabriusculis; antheris valde exsertis 0.6 cm. longis glabris; ovario ovoideo ca. 0.1 cm. longo glabriusculo; stigmatibus 0.15 cm. longo; nectariis conrescentibus membranaceis margine anguste lobatis ca. 0.15 cm. longis ovarium omnino superantibus; folliculis teretibus falcatis 30–50 cm. longis ca. 0.4–0.5 cm. diametro metientibus apice saepe conrescentibus glabris; seminibus 1.5–1.8 cm. longis como dilute luteo ca. 2.5 cm. longo.

Fruticose lianas; stems rather stout, terete, glabrous, warty-lenticellate when fully mature; leaves shortly petiolate, broadly obovate-elliptic, apex shortly and acutely acuminate, base obtusely cuneate, 18–25 cm. long, 8–10 cm. broad, firmly membranaceous, glabrous throughout; petioles 1.0–1.5 cm. long; stipular appendages interpetiolar, numerous, narrowly dentiform; inflorescence lateral, twice- to thrice-dichotomous, bearing several yellowish flowers; peduncle (somewhat after maturity) 5.5–6.0 cm. long, glabrous, warty-lenticellate; pedicels 0.9–1.2 cm. long, minutely papillate (?); calyx-lobes rather

broadly elliptic, obtusish to rather broadly acute, 0.7–0.9 cm. long, subcoriaceous, pale green, evidently not suffused with purple, minutely papillate without and within, the squamellae relatively small, acuminate; corolla salverform, the tube 1.8–2.0 cm. long, about 0.2–0.225 cm. in diameter at the base, glabrous without, minutely puberulent within near the attachment of the stamens, otherwise glabrous, the internal appendages linear, entire, somewhat exserted, the orifice callose-annulate, the lobes obliquely obovate, minutely acuminate, 1.2–1.3 cm. long, very minutely papillate without, essentially glabrous within; anthers exserted, 0.6 cm. long, glabrous; ovary ovoid, about 0.1 cm. long, essentially glabrous; stigma 0.15 cm. long; nectaries concrescent, membranaceous, the margin narrowly and minutely lobed, about 0.15 cm. long, completely concealing the ovary; follicles terete, falcate, usually united at the tips, 30–50 cm. long, about 0.4–0.5 cm. in diameter, glabrous; seeds 1.5–1.8 cm. long, the pale yellow coma about 2.5 cm. long.

GUATEMALA: Sepacuite, Oct., 1901, *Owen 1* (US, TYPE, MBG, photograph); SANTA ROSA: Volcan Tecuamburro, alt. 2000 m., Febr., 1893, *Heyde & Lux 4539* (G).

Closely related to *P. portobellensis*, differing chiefly in the calyx-lobes, squamellae, and more extensive inflorescence. *Heyde & Lux 4539* is unfortunately long past prime and rather fragmentary; its relegation to this species is therefore somewhat uncertain.

**44. *Prestonia portobellensis*** (Beurl.) Woodson, Ann. Mo. Bot. Gard. 18: 553. 1931.

*Echites portobellensis* Beurl. Vet. Akad. Handl. Stockh. 137. 1854 (1856).

*Haemadictyon schizadenium* Muell.-Arg. Linnaea 30: 431. 1860; Miers, Apoc. So. Am. 261. 1878.

*Prestonia schizadenia* (Muell.-Arg.) Hemsl. Biol. Centr.-Am. Bot. 2: 312. 1881.

*Prestonia (Haemadictyon) macrocarpa* Hemsl. loc. cit. 311. 1881.

Stems relatively stout, minutely scabridulous in the vicinity of the nodes, conspicuously lenticellate when fully mature; leaves oblong-elliptic, apex obtuse to abruptly and shortly acu-

minate, base obtuse or rounded, 9–29 cm. long, 3–18 cm. broad, firmly membranaceous to subcoriaceous, glabrous, opaque, or slightly nitidulous above; petioles 0.6–3.0 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence subcorymbose, di- or trichotomous, less frequently simple, bearing 8–30 purplish-yellow flowers; peduncle much shorter than the subtending leaves, glabrous; pedicels 0.6–1.8 cm. long, somewhat accrescent after maturity, glabrous or very minutely papillate; bracts ovate-lanceolate, 0.05–0.4 cm. long, scarious or slightly foliaceous; calyx-lobes oblong-elliptic, acuminate, 1.1–1.7 cm. long, coriaceous or subcoriaceous, more or less flushed with purplish, glabrous or very minutely and indistinctly papillate, the squamellae dentiform-deltoid, very minutely erose; corolla salverform, glabrous or very minutely papillate without, the tube 1.1–1.7 cm. long, about 0.3–0.35 cm. in diameter at the base, epistaminal appendages slightly exserted or at least attaining the faucal annulus, 0.2–0.4 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 1.0–1.5 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers slightly exserted, narrowly oblong-sagittate, slightly pandurate, 0.5–0.6 cm. long, puberulent-papillate to minutely papillate dorsally; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.15 cm. long; nectaries wholly concrescent, thin and somewhat diaphanous, not thick and fleshy, minutely erose or lacerate, conspicuously surpassing the ovary; follicles relatively long and stout, 33–35 cm. long, continuous, somewhat falcate, often united at the tips, glabrous; seeds 1.5–1.6 cm. long, the pale yellowish coma 2.5–3.7 cm. long.

MEXICO: OAXACA: vicinity of Cafetal Concordia, alt. 400–650 m., April 1–15, 1933, *Morton & Makrinus 2348* (US).

HONDURAS: ATLANTIDA: beside the trail, above Lancetilla, alt. 200 ft., July 15, 1934, *Yunker 4596* (Herb. Univ. Mich.).

SALVADOR: SONSONATE: vicinity of Sonsonate, alt. 220–300 m., March 18–27, 1922, *Standley 22349* (G).

COSTA RICA: LIMON: Moin Hill, près Limon, June, 1898, *Pittier 12401* (G, V); Pinta près Limon, litt. Atlantique, Sept., 1899, *Pittier 18016* (B, G); PUNTARENAS: forêts de Santo Domingo de Golfo Dulce, March, 1896, *Pittier 9935* (BB, Bx); environs de Sto. Domingo de Osa, March, 1896, *Tondus 9889* (Bx, V).

PANAMA: COLON: Portobello, in silvis ad littora, April, 1826, *Billberg s.n.* (S. TYPE, MBG, photograph and analytical drawings); Santa Rita trail, Febr. 27, 1905, *Cowell 105* (NY); Chagres, Jan.-March, 1850, *Fendler 250* (MBG, V); Gatun Sta., Jan. 28, 1860, *Hayes 450* (NY).

Remarks on this species and its nomenclature will be found in *Ann. Mo. Bot. Gard.* 18: 553-554. 1931. The species is not a very uniform nor constant one as interpreted above, and may require segregation at a future date.

**45. *Prestonia lacerata* Woodson, spec. nov.**

Fruticosa volubilis altitudine ignota; ramulis gracilibus glaberrimis maturitate conspicue lenticellatis; foliis oblongo-ellipticis apice abrupte acuminato-mucronatis basi late obtusis 12-20 cm. longis 5.5-9.5 cm. latis firmiter membranaceis subcoriaceisve glaberrimis supra sublutescentibus subtus opacis; petiolis 1.0-1.5 cm. longis; appendicibus stipulaceis interpetiolaribus numerosis minute dentiformibus vix bene visis; inflorescentiis corymbosis dichotome divisis flores gilvos 30-40 gerentibus; pedunculo foliis ca. dimidio brevior minute puberulo; pedicellis 1.2-1.3 cm. longis post maturitatem paulo accrescentibus minute ferrugineo-puberulis; bracteis acuminato-deltoides scariaceis vix 0.1 cm. longis; calycis laciniis oblongo-lanceolatis acute acuminatis 1.0-1.1 cm. longis membranaceis foliaceis post exsiccationem paulo purpurisatis sparse minuteque pilosulis glabratissive squamellis subtrigonalibus acutis integris; corollae salverformis tubo 1.5 cm. longo basi ca. 0.18-0.2 cm. diametro metiente extus sparse minuteque puberulo-papillato intus prope insertionem staminum molliter puberulo appendicibus epistaminalibus linearibus ca. 0.35 cm. longis paulo exsertis annulo faucium conspicue incrassato lobis oblique obovato-dolabriformibus 0.9 cm. longis patentibus; antheris oblongo-sagittatis 0.5 cm. longis dorso minute puberulis apice exsertis; ovario ovoideo ca. 0.15 cm. longo glabro; stigmatibus subcapitato-fusiforme 0.15 cm. longo; nectariis basi concretescentibus ubique aliquid incrassatis caeterumque delicate membranaceis purpurisatisque hyalinis margine profunde irregulariterque laceratis ovarium ca. dimidio superantibus; folliculis gracilibus continuis falcatis 30-45 cm.

longis glaberrimis; seminibus immaturis 1.8–2.0 cm. longis como dilute aurantiaco ca. 4 cm. aequante.

Stems relatively slender, glabrous, conspicuously lenticellate at maturity; leaves oblong-elliptic, apex abruptly acuminate-mucronate, base broadly obtuse, 12–20 cm. long, 5.5–9.5 cm. broad, firmly membranaceous to subcoriaceous, glabrous, somewhat lustrous above, opaque beneath; petioles 1.0–1.5 cm. long; stipular appendages interpetiolar, numerous, minutely dentiform; inflorescence corymbose, dichotomously divided, bearing 30–40 pale yellowish flowers; peduncle about half as long as the subtending leaves, very minutely ferruginous-puberulent; pedicels 1.2–1.2 cm. long, somewhat accrescent at maturity, minutely ferruginous-puberulent; bracts acuminate-deltoid, scarious, less than 0.1 cm. long; calyx-lobes oblong-lanceolate, acutely acuminate, 1.0–1.1 cm. long, membranaceous, foliaceous (somewhat suffused with purple in desiccation), sparsely and minutely pilosulose to glabrate without, the squamellae subtrigonal, acute, entire; corolla salverform, the tube 1.5 cm. long, about 0.18–0.2 cm. in diameter at the base, sparsely and minutely puberulent-papillate without, softly puberulent near the insertion of the stamens within, epistaminal appendages linear, about 0.35 cm. long, slightly exserted, faucal annulus conspicuously thickened, the lobes obliquely obovate-dolabriform, 0.9 cm. long, reflexed; anthers oblong-sagittate, 0.5 cm. long, minutely puberulent dorsally, the tips slightly exserted; ovary ovoid, about 0.15 cm. long, glabrous; stigma subcapitate-fusiform, 0.15 cm. long; nectaries about twice surpassing the ovary, concrescent and somewhat incrassate at the base, membranaceous and purplish-hyaline above, deeply and irregularly lacerate; follicles slender, continuous, falcate, 30–45 cm. long, glabrous; seeds (immature) 1.8–2.0 cm. long, the pale tawny coma about 4 cm. long.

PERU: LORETO: Regenwald, Iquitos, alt. 100 m., May 12, 1925, *Tessmann 5106* (B, TYPE, MBG, photograph and analytical drawings).

Unique among the South American *Prestonias* because of the subpetalaceous nectary of the flowers, by which it simulates the Central American species of § *Annulares*.



Sect. 4. TOMENTOSAE Woodson. Relatively stout, usually densely ferruginous-pubescent lianas; leaves membranaceous to subcoriaceous; inflorescence simple or variously compound, typically bostrychoid-racemose to subumbellate; calyx-lobes relatively large and conspicuously foliaceous; corolla salverform, rarely infundibuliform, more or less densely pubescent without, appendiculate or exappendiculate within, the epistaminal appendages occasionally replaced by callous ridges, the faucal annulus conspicuously thickened or tuberculate; anthers included or the tips more or less exserted. Spp. 46-60.

This is the most difficult section of *Prestonia*. Since the delimitation of the species appears rather vague and confusing in certain instances, in spite of the relatively large number of herbarium specimens available for study, an endeavor has been made to maintain conservatively the specific limits recognized by previous botanists. Subsequent study, particularly if supplemented by extensive field observation, may well differ in this regard. It is scarcely to be avoided that our present conceptions of taxonomic units in the Apocynaceae, as in other tropical American groups, should be other than purely elemental.

In several instances in the delimitation of the species to follow, the color of the indument has appeared significant. Here the difficulty of ascribing intelligibly the color to desiccated specimens has been considerable, and doubtless will be found unsatisfactorily anticipated in many instances. It should be borne in mind that the color of the indument, described as such, refers in all instances to the collective color of the trichomes themselves, and not, for instance, to the gross shade of the indument viewed in conjunction with a variable background of leaf- or stem-surface, which would necessarily vary greatly according to the relative density of the trichomes and the consequently varying proportion of the vegetative ground tissue visible.

#### KEY TO THE SPECIES

A. Corolla-tube appendiculate within.

B. Epistaminal appendages exserted, or at least attaining the faucal annulus.

- C. Inflorescence dichotomous, occasionally rather obscurely so; foliar indument very finely velutinous, umber-brown, opaque.....46. *P. surinamensis*
- CC. Inflorescence simple, or rarely very obscurely compound.
- D. Calyx-lobes as long as the corolla-tube, or nearly so; inflorescence many-flowered.
- E. Anthers glabrous.
- F. Foliar indument dull yellowish- or buffy-brown, opaque, or scarcely lustrous; calyx tomentulose, subappressed; plants of northern Colombia to south-central Brazil and Paraguay .....47. *P. tomentosa*
- FF. Foliar indument dark orange-brown, lustrous; calyx hispid-hirsute to -hirsutulose.
- G. Foliar indument velutinous; calyx hispid-hirsutulose; plants of southeast-central Brazil.....48. *P. bahiensis*
- GG. Foliar indument hispid to hispidulose, much sparser than in the preceding; calyx hispid-hirsute; plants of Panama to French Guiana.....49. *P. ipomaeifolia*
- EE. Anthers pubescent, at least puberulent-papillate dorsally.
- F. Corolla-tube 1.6–2.0 cm. long, appressed-villosulose without, the lobes 1.2–1.5 cm. long; nectaries surpassing the ovary; plants of southern Brazil and adjacent Paraguay.....50. *P. calycina*
- FF. Corolla-tube 2.0–2.2 cm. long, minutely puberulent without, the lobes 2.0–2.2 cm. long; nectaries about half equalling the ovary; plants of Peru.....51. *P. cordifolia*
- DD. Calyx-lobes about half as long as the corolla-tube; inflorescence few-flowered.....52. *P. brachypoda*
- BB. Epistaminal appendages deeply included.
- C. Inflorescence simple, or essentially so, subumbellate; corolla 2.0–2.3 cm. long; anthers barely included.....53. *P. mucronata*
- CC. Inflorescence repeatedly dichotomous, corymbose or thyrsiform; corolla 1.0–1.3 cm. long; anther-tips exerted.....54. *P. parviflora*
- AA. Corolla-tube exappendiculate within, or with callous ridges or protuberances in the position of epistaminal appendages.
- B. Follicles very short and stout, napiform, sharply divaricated; species of Mexico and Central America.
- C. Corolla salverform, the tube not dilating above the insertion of the stamens, or scarcely so.
- D. Nectary annular, broadly 5-lobed, or essentially entire, about equalling or barely surpassing the ovary.
- E. Corolla 3.5–4.0 cm. long; epistaminal protuberances linear, 0.2–0.25 cm. long; plants of southern Mexico and Guatemala....55. *P. mexicana*
- EE. Corolla 2.8–3.0 cm. long; epistaminal protuberances nearly quadrate, 0.1–0.15 cm. long; plants of British Honduras.....56. *P. amanuensis*
- DD. Nectary tubular or subtubular, deeply 5-lobed, conspicuously surpassing the ovary; corolla 4.0–4.5 cm. long; plants of Costa Rica.....57. *P. isthmica*

- CC. Corolla infundibuliform, the tube conspicuously dilated above the insertion of the stamens.....58. *P. speciosa*
- BB. Follicles relatively long and slender, not divaricate; species of South America.
- C. Inflorescence relatively lax and elongate; anthers included, sparsely pilose.....59. *P. Riedelia*
- CC. Inflorescence congested, subumbellate; anther-tips exserted, glabrous .....60. *P. Schumanniana*

**46. *Prestonia surinamensis* Muell.-Arg. Linnaea 30: 433. 1860; Miers, Apoc. So. Am. 147. 1878.**

Stems relatively stout, densely and minutely ferruginous-tomentose, eventually becoming glabrate; leaves broadly ovate to ovate-elliptic, apex shortly and abruptly acuminate, base obtuse to rounded, 10-24 cm. long, 6-17 cm. broad, firmly membranaceous, uniformly and very densely velutinous when young, densely and very finely velutinous beneath, above minutely scabridulous to glabrate generally, pilosulose along the midrib and veins when fully mature, the indument dull umber-brown, opaque, not lustrous; petioles 0.7-3.5 cm. long, densely ferruginous-pubescent; stipular appendages interpetiolar, numerous, pectinate-flagelliform, more or less ferruginous-pilosulose; inflorescence corymbose, dichotomous, occasionally rather obscurely so, bearing 10-40 whitish-yellow flowers; peduncle minutely ferruginous-velutinous, much shorter than the subtending leaves; pedicels 0.4-0.7 cm. long, somewhat accrescent after maturity, minutely ferruginous-velutinous; bracts ovate-lanceolate, somewhat foliaceous, 0.6-0.8 cm. long; calyx-lobes broadly ovate- to oblong-elliptic, shortly acuminate to acute, 0.8-1.2 cm. long, foliaceous, minutely appressed ferruginous-velutinous, the internal squamellae broadly dentiform-ligular, emarginate, somewhat pilosulose; corolla salverform, densely ferruginous-villosulose without, the tube 1.5-1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages slightly exserted or at least attaining the orifice, 0.2-0.4 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.6-0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers barely exserted, oblong-sagit-

tate, 0.6–0.7 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous or essentially so; stigma 0.1–0.15 cm. long; nectaries concrescent, rather irregularly 5-cleft or essentially entire, fleshy, conspicuously surpassing the ovary; follicles very stout and rigid, narrowly napiform, sharply divaricate, 9–11 cm. long, minutely ferruginous-velutinous to glabrate; seeds 1.4–1.7 cm. long, the pale tawny coma 2.0–3.2 cm. long.

BRITISH GUIANA: upper Rupununi River, near Dadanawa, May 30, 1922, *Crus* 1419 (MBG, NY); same locality, June 10, 1922, *Crus* 1489 (MBG, NY).

DUTCH GUIANA: Plantatio Beekhuizen, date lacking, *Wulfschlägel* 1039 (Bx, V); exact locality and date lacking, *Hostmann* 981 (B, U, V, TYPE, MBG, photograph and analytical drawings); fluv. Tapanahoni, Aug., 1904, *Versteeg* 753 (U); fluv. Gonimi, Aug., 1903, *Versteeg* 72 (U).

BRAZIL: PARA: insula Mexiana, in fauce Amazonum fluvii, Sept. 20, 1901, *Guedes* 21640 (B); Rio Branco de Obidos, ad ripas fluminis, Jan. 28, 1918, *Ducke* 21628 (B); Ourem, Rio Gnaura, Dec. 4, 1903, *Siqueira* 21633 (B).

**47. *Prestonia tomentosa*** R. Br. Mem. Wern. Soc. 1: 70. 1811; A. DC. in DC. Prodr. 8: 429. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 163. 1860; Miers, Apoc. So. Am. 144. *pl.* 20B. 1878.

*Prestonia latifolia* Benth. in Hook. Jour. Bot. 3: 250.

1841; A. DC. loc. cit. 429. 1844; Miers, loc. cit. 145. 1878.

*Prestonia lutescens* Muell.-Arg. loc. cit. 164. 1860; Miers, loc. cit. 147. 1878.

*Prestonia lanata* Muell.-Arg. loc. cit. 1860; Miers, loc. cit. 1878.

*Prestonia Cearensis* Miers, loc. cit. 148. 1878.

*Prestonia sericocalyx* Malme, Bihang till K. Sv. Vet. Akad. Handl. Afd. III. 24<sup>10</sup>: 29. 1899.

Stems relatively stout, densely and rather pale ferruginous-tomentose, eventually becoming glabrate; leaves broadly ovate, apex shortly acuminate, base broadly obtuse to rounded, infrequently very obscurely cordate, 8–19 cm. long, 5–12 cm. broad, firmly membranaceous, above rather sparsely and minutely ferruginous-hirtellous, more densely so along the midrib and veins, beneath densely and rather closely velutinous-tomentose, the indument dull yellowish- or buffy-brown, opaque, not lustrous; petioles 0.3–1.2 cm. long, minutely ferruginous-tomentose as upon the stem; stipular appendages interpetiolar,

pectinate-flagelliform, somewhat ferruginous-pilosulose at the base; inflorescence subumbellate, simple, bearing 10–30 waxy, yellow flowers; peduncle much shorter than the subtending leaves, pale ferruginous-tomentulose; pedicels 0.4–1.0 cm. long, somewhat accrescent after maturity, minutely ferruginous-tomentulose as upon the peduncle; bracts ovate-lanceolate, 0.8–1.8 cm. long, slightly foliaceous; calyx-lobes oblong- to ovate-elliptic, acute to acuminate, 1.0–1.8 cm. long, foliaceous, subappressed-tomentulose, the internal squamellae broadly dentiform, entire or very minutely erose; corolla salverform, densely and appressed ferruginous-villous without, the tube 1.5–1.8 cm. long, about 0.3–0.35 cm. in diameter at the base, epistaminal appendages barely exserted, or about attaining the orifice, 0.15–0.4 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 0.7–1.2 cm. long, reflexed or widely spreading; stamens inserted at about midway or the upper  $\frac{1}{3}$  of the corolla-tube, the anthers barely exserted, sagittate, 0.5–0.6 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, minutely puberulent-papillate; stigma 0.05–0.1 cm. long; nectaries concrescent, broadly and rather shallowly 5-lobed, fleshy, conspicuously surpassing the ovary; follicles stout and rigid, narrowly napiform, sharply divaricate, 6–9 cm. long, densely ferruginous-hispid; seeds 0.8–0.9 cm. long, the pale tawny coma 3.5–4.2 cm. long.

COLOMBIA: MAGDALENA: growing over a shrub on open, low grassland by a forest-lined stream, near Jordan, alt. 800 ft., Nov. 5, 1898, *H. H. Smith 165* (NY).

VENEZUELA: MERIDA: a few miles s. of Guigue, alt. 2000 ft., Jan. 25, 1855, *Fendler 1052* (G); Mariara, alt. 450 m., Sept., 1899, *Preuss 1617* (B).

BRITISH GUIANA: savannah, Pirara, date lacking, *Schomburgk 755* (B, Camb., K, NY, V); Pirara, 1841–2, *Schomburgk 374* (DL, V).

BRAZIL: AMAZONAS: bei der Serra do Stel., Rio Branco; Surumu, Nov., 1909, *Ule 8266* (B, DL); am Igarape Imclu bei Pracana, Rio Branco, Surumu, Febr. 1909, *Ule 7939* (B, DL); Boá Vista, Rio Branco super., silvula secundaria, July 1913, *Kuhlmann 3646* (B); MATTO GROSSO: Coxipo, prope Cuyaba, in margine silvula non in "cerrado," Dec. 27, 1893, *Molme 1276B* (DL, S); MINAS GERAES: exact locality and date lacking, *Claussen s.n.* (DL); RIO DE JANEIRO: Palmita, date lacking, *Pohl 2214* (Bx, V); exact locality and date lacking, *Glasiou 8800* (Bx); Rio de Janeiro, 1910, *Luetszelburg s.n.* (B, M); SÃO PAULO: Rincão, Jan. 25, 1928, *Toledo 23550* (B); DATA INCOMPLETE: *Pohl s.n.* (Bx); *Claussen 339* (B, BB); *Glasiou 19625* (B).

PERU: LORETO: Tarapoto, Dec., 1902, *Ule 6650* (B, DL).

BOLIVIA: LA PAZ: Ixiamas, alt. 800 ft., Dec. 17, 1921, *Cardeñas 1928* (NY); SANTA CRUZ: im Wald zwischen Rio Pirai und Rio Cuchi bei Santa Cruz, Jan., 1911, *Herzog 1514* (B, S, V).

PARAGUAY: collines herbeuses entre le Cerro-Hu et le Cerro San Tomas, près Paraguarí, Jan. 31, 1877, *Balansa 1376* (Bx, DL); in capueras Caaguazu, date lacking, *Jørgensen 4708* (MBG); Villa Concepcion, Febr., 1896, *Anisits s.n.* (S); Cordillera de Altos, Cerro Chochi, Dec. 1902, *Fiebrig 640* (B, DL); Wald, Cordillera de Altos, Dec., 1902, *Fiebrig 647* (B); zwischen Rio Apa und Rio Aquidaban, Centurion, Jan., 1909, *Fiebrig 1463* (B); in regione lacus Ypacaray, Febr., 1913, *Hassler 11547* (B, DL, MBG); in regione cursus superioris fluminis Apa, Nov., 1901, *Hassler 7820* (B, BB, V).

**48. *Prestonia bahiensis* Muell.-Arg. in Mart. Fl. Bras. 6: 164. 1860; Miers, Apoc. So. Am. 147. 1878.**

Stems relatively stout, densely ferruginous-tomentose, eventually becoming glabrate; leaves broadly oval to oblong-elliptic, apex acuminate to obtuse, base very broadly obtuse or rounded, occasionally very obscurely cordate, 5–16 cm. long, 3.0–7.5 cm. broad, firmly membranaceous, above ferruginously hispid-hirtellous, beneath densely velutinous, the indument dark orange-brown, very lustrous; petioles 0.3–1.0 cm. long, indument as upon the stem; stipular appendages intrapetiolar, several, pectinate-flagelliform, ferruginous-pilosulose, relatively inconspicuous; inflorescence densely subumbellate, simple, bearing 10–30 yellowish flowers; peduncle much shorter than the subtending leaves, indument as on the stem; pedicels 0.4–1.0 cm. long, somewhat accrescent after maturity, ferruginous-tomentulose; bracts linear-lanceolate, 0.7–1.2 cm. long, slightly foliaceous; calyx-lobes ovate-lanceolate, acuminate, densely hispid-hirsutulose, foliaceous, the internal squamellae dentiform-ligular, entire or very minutely erose, minutely pilosulose; corolla salverform, densely ferruginous-villosulose without, the tube 1.5–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages slightly exserted, 0.25–0.3 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 0.7–0.9 cm. long; stamens inserted somewhat above midway within the corolla-tube, the anthers barely exserted, oblong-sagittate, 0.55–0.6 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, papillate or essentially glabrous; stigma 0.1–0.15 cm.

long; nectaries concrescent, more or less deeply lobed or cleft, fleshy, conspicuously surpassing the ovary; follicles unknown.

BRAZIL: BAHIA: S. Thome, June, 1844, *Blanchet 3776* (BB, Bx, TYPE, DC, MBG, photograph and analytical drawings); MINAS GERAIS: Lagoa Santa, 1870, *Warming s.n.* (DC); inter Ponte do Sapucahy et Retero, Jan. 23, 1868, *Regnell III 1600* (B, S); Campo Corrego do Leitão, Belo Horizonte, Aug., year lacking, *Gehrt 3183* (B); Sabara, Jan., 1916, *Hoehne 6874* (B); exact locality and date lacking, *Clausen s.n.* (V); SÃO PAULO: Magy Mirim, March 20, 1874, *Mosen 1461* (S); DATA INCOMPLETE: *Sellow 1406* (B).

49. *Prestonia ipomaeifolia* A. DC. in DC. Prodr. 8: 429. 1844; Miers, Apoc. So. Am. 145. 1878.

*Prestonia Seemannii* Miers, loc. cit. 146. 1878.

Stems relatively slender, somewhat laxly ferruginous-pilose; leaves broadly elliptic to oval, apex very abruptly and shortly acuminate, base broadly obtuse or rounded, 9–14 cm. long, 5–8 cm. broad, firmly membranaceous, above rather sparsely and uniformly hispid-hirtellous, beneath somewhat more densely hispid to hispidulose, the indument dark orange-brown, lustrous; petioles 0.4–0.6 cm. long, indument as on the stem; stipular appendages intrapetiolar, numerous, narrowly pectinate-flagelliform, ferruginous-pilose at the base, relatively conspicuous; inflorescence densely subumbellate, simple, bearing 10–30 yellowish flowers; peduncle much shorter than the subtending leaves, indument as on the stem; pedicels 0.4–0.7 cm. long, somewhat accrescent after maturity, ferruginous-hirtellous; bracts ovate-lanceolate to linear-lanceolate, 0.7–0.9 cm. long, somewhat foliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.9–1.1 cm. long, somewhat foliaceous, 0.9–1.1 cm. long, hispid-hirsute, the internal squamellae broadly dentiform, minutely erose; corolla salverform, densely ferruginous-villous without, the tube 1.7–1.8 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages barely exerted, or about attaining the orifice, 0.15 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 1.2–1.4 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers slightly exerted, oblong-sagittate, 0.6 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, essentially glabrous;

stigma 0.1 cm. long; nectaries conerescent, tubular, barely 5-lobed, fleshy, conspicuously surpassing the ovary; follicles unknown.

PANAMA: PANAMA: Camino del Boticario, near Chepo, alt. 30–50 m., Oct., 1911, *Puttier 4700* (G, US).

COLOMBIA: MAGDALENA: Sta. Isabel de Hungaria bei Tucurinca, alt. ca. 150 m., Oct. 16, 1926, *Schultze 605* (B).

FRENCH GUIANA: Cayenne, date lacking, *le Blond s.n.* (DC, TYPE).

50. *Prestonia calycina* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 162. 1860; Miers, Apoc. So. Am. 146. 1878, not Lindl.

*Prestonia hirsuta* Muell.-Arg. loc. cit. pl. 48. 1860; Miers, loc. cit. 147. 1878, not Spreng.

Stems relatively stout, coarsely ferruginous-hirsute to glabrate; leaves broadly oval to oblong-elliptic, apex very abruptly and shortly acuminate to obtuse or rounded, base broadly obtuse or rounded to obscurely cordate, 9–17 cm. long, 6–13 cm. broad, firmly membranaceous, above appressed ferruginous-hispidulous to scabridulous, occasionally essentially glabrate, beneath densely ferruginous-tomentulose, rarely glabrate; petioles 0.5–1.1 cm. long, ferruginous-tomentulose to glabrate; stipular appendages interpetiolar, numerous, rather broadly pectinate; inflorescence subumbellate, simple, bearing 6–18 yellowish flowers; peduncle much shorter than the subtending leaves, indument as upon the stem; pedicels 0.3–1.0 cm. long, ferruginous-tomentulose to glabrate; bracts ovate to ovate-lanceolate, 0.7–1.4 cm. long, foliaceous; calyx-lobes ovate to oblong-lanceolate, acuminate, 1.2–1.8 cm. long, foliaceous, ferruginous-hirtellous, the internal squamellae irregularly erose or lacerate, sparsely pilosulose; corolla salverform, densely and appressed ferruginous-villosulose, the tube 1.6–2.0 cm. long, about 0.3–0.35 cm. in diameter at the base, epistaminal appendages barely exerted, or about attaining the orifice, 0.25–0.4 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 1.2–1.5 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers barely exerted, oblong-sagittate, 0.5–0.7 cm. long, more or less puberulent dorsally, rarely nearly glabrate; ovary ovoid, about



0.15 cm. long, glabrous; stigma 0.1–0.15 cm. long; nectaries crescent, broadly tubular, more or less deeply 5-lobed, fleshy, conspicuously surpassing the ovary; follicles stout and rigid, narrowly napiform, sharply divaricate, 6.5–7.0 cm. long, retrorsely hirtellous to obsoletely scabridulous; seeds 1.1–1.2 cm. long, the pale tawny coma 3.0–3.5 cm. long.

BRAZIL: RIO DE JANEIRO: Cantogallo, 1861, *Peckholt 559* (Bx); exact locality lacking, *Beyrich s.n.* (B); *Glaziov 12944* (B); *Glaziov 8173* (B); DATA INCOMPLETE: *Pohl 5167* (V, MBG, photograph and analytical drawings); *Sellow 550* (B); *Glaziov 18363* (B).

PARAGUAY: in regione cursus superioris fl. Y-aca, Dec., 1900, *Hassler 6776* (B, BB, V).

*Hassler 6776* is more nearly glabrate than the majority of the Brazilian representatives, but is surpassed in this respect by *Glaziov 18363*, from an unspecified locality in Brazil. The specimens cited appear conspecific in all essential respects.

#### 51. *Prestonia cordifolia* Woodson, spec. nov.

Ut creditur suffruticosa vel fruticosa volubilis; ramulis sat gracilibus dense ferrugineque puberulo-tomentulosis; foliis oppositis manifeste petiolatis ovatis vel ovato-ellipticis apice abrupte acuminatis basi conspicue cordatis superne late obtusis rotundatisve 6–12 cm. longis 4–9 cm. latis firmiter membranaceis supra minute scabridulo-puberulis subtus dense ferrugineo-tomentulosis; petiolis 1.3–1.5 cm. longis ut in ramulo vestitis; appendicibus stipulaceis interpetiolaribus inconspicue dentiformibus utroque latere 3–4; inflorescentiis simplicibus corymbosis foliis multo brevioribus flores (ut creditur aut gilvos aut flavos) 8–10 gerentibus; pedunculo dense ferrugineo-tomentuloso petiolis subaequante; pedicellis 1.0–1.2 cm. longis ut in pedunculo vestitis; bracteis oblongo-lanceolatis 1.0–1.5 cm. longis foliaceis minute ferrugineo-puberulis; calycis laciniis ovato-oblongis abrupte acuminatis basi usque  $\frac{1}{3}$  altitudinem connatis 2.0–2.2 cm. longis extus leviter intusque minute ferrugineo-puberulis squamellis inconspicuis late triangulo-deltiformibus integerrimis apice obtusis ca. 0.05 cm. longis minutissime puberulis; corollae salverformis tubo 2.0–2.2 cm. longo basi ca. 0.18–0.2 cm. diametro

metiente faucibus 0.25–0.3 cm. diametro metientibus extus omnino minute ferrugineo-puberulo intus supra insertionem staminum retrorse pilosulo appendicibus epistaminalibus oblongis 0.45–0.5 cm. longis conspicue exsertis annulo faucium manifeste incrassato, lobis oblique obovato-oblongis 2.0–2.2 cm. longis patentibus extus minute ferrugineo-puberulis intus glabris; staminibus prope fauces insertis antheris conspicue exsertis lanceolato-sagittatis 0.7–0.75 cm. longis dorso minute hispidulis; stigmatе oblongo-subcapitato 0.17 cm. longo; ovario ovoido ca. 0.2 cm. longo glabro; nectariis concrescentibus haud conspicue lobatis incrassatis ovarium ca. dimidio aequantibus; folliculis ignotis.

Stems relatively slender, densely ferruginous-tomentulose; leaves opposite, petiolate, ovate to ovate-elliptic, apex abruptly acuminate, base conspicuously cordate to broadly obtuse or rounded above, 6–12 cm. long, 4–9 cm. broad, firmly membranaceous, above minutely scabridulous-puberulous, beneath densely ferruginous-tomentulose; petioles 1.3–1.5 cm. long, minutely ferruginous-tomentulose; stipular appendages interpetiolar, inconspicuously dentiform, 3–4 upon either side of the node; inflorescence simple, corymbose, much shorter than the leaves, bearing 8–10 (probably yellowish or cream-colored) flowers; peduncle densely ferruginous-tomentulose, about equalling the subtending petioles; pedicels 1.0–1.2 cm. long, the indument as upon the peduncle; bracts conspicuously foliaceous, oblong-lanceolate, 1.0–1.5 cm. long, very minutely ferruginous-puberulous; calyx-lobes ovate-oblong, abruptly acuminate, connate at the base for about  $\frac{1}{3}$  their length, 2.0–2.2 cm. long, conspicuously foliaceous, without softly and densely, within minutely ferruginous-puberulous, the squamellae broadly triangular-deltiform, entire, the apex broadly obtuse, about 0.05 cm. long, very minutely puberulent; corolla salverform, the tube 2.0–2.2 cm. long, about 0.18–0.2 cm. in diameter at the base and 0.25–0.3 cm. in diameter at the orifice, minutely ferruginous-hirtellous or -puberulous without, retrorsely pilosulose within above the insertion of the stamens, epistaminal appendages oblong, 0.45–0.5 cm. long, conspicuously

exserted, faucal annulus conspicuously thickened; lobes obliquely obovate-oblong, 2.0–2.2 cm. long, reflexed, without minutely ferruginous-puberulent, within glabrous; stamens inserted near the orifice of the corolla-tube, the anthers conspicuously exserted, lanceolate-sagittate, 0.7–0.75 cm. long, minutely hispidulous dorsally; ovary ovoid, about 0.2 cm. long, glabrous; stigma oblong-subcapitate, 0.17 cm. long; nectaries conerescent, scarcely lobed, greatly thickened, about half equalling the ovary; follicles unknown.

PERU: CAJAMARCA: Catache, Piov. Contumaza, alt. 5000 ft., May 27, 1875, *Ramond* 8238 (B, TYPE, MBG, photograph and analytical drawings).

Closely related to *P. calycina* Muell.-Arg., but differing, in addition to the key characters, in such features as the vegetative induments, stipular appendages, length and degree of connation of calyx-lobes, and character of the squamellae.

**52. *Prestonia brachypoda* Blake, Contr. U. S. Nat. Herb. 20: 530. 1924.**

Stems relatively stout, ferruginous-velutinous when young, soon becoming scabridulous to glabrate; leaves broadly obovate-oblong, apex obtuse to rounded, base obscurely cordate, 14–25 cm. long, 9–12 cm. broad, firmly membranaceous, above sparsely ferruginous-pilosulose, beneath densely and minutely ferruginous-velutinous; petioles 0.3–0.5 cm. long, very minutely ferruginous-vellutinous; stipular appendages interpetiolar, numerous, pectinate-flagelliform, sparsely and minutely pilosulose; inflorescence densely subumbellate-capitate, simple, bearing 3–6 yellowish flowers; peduncle extremely short, scarcely surpassing the subtending petioles, ferruginous-pubescent; pedicels 0.7–0.8 cm. long, minutely appressed-puberulent; bracts linear-lanceolate, long-acuminate, 0.4–0.6 cm. long, slightly foliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.8–0.9 cm. long, somewhat foliaceous, minutely appressed-puberulent, the internal squamellae broadly dentiform-ligular, entire or very minutely erose or emarginate; corolla salverform, appressed ferruginous-villosulose without, the tube 1.5–1.7 cm. long, about 0.25 cm. in diameter at the base, epistaminal

appendages slightly exserted, 0.3–0.35 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, shortly acuminate, 0.6–0.7 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers barely exserted, oblong-sagittate, 0.5 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous; stigma 0.1–0.15 cm. long; nectaries concrescent, somewhat fleshy, tubular or subtubular, broadly 5-lobed, conspicuously surpassing the ovary; follicles unknown.

VENEZUELA: CARABOBO: Guaremales, road from Puerto Cabello to San Felipe, in forest, alt. 10–100 m., May 15–29, 1920, *Pether 8832* (G, US, TYPE, MBG, photograph and analytical drawings).

**53. *Prestonia mucronata* Rusby, Descr. So. Am. Pl. 90. 1920.**

Stems relatively slender, densely and minutely ferruginous-tomentose, eventually becoming glabrate when fully mature; leaves broadly oval, apex very abruptly and shortly acuminate, base broadly obtuse or rounded, 4–8 cm. long, 3–5 cm. broad, firmly membranaceous, above rather sparsely and minutely ferruginous-hispidulose, beneath minutely and rather sparsely ferruginous-hirtellous; petioles 0.7–1.5 cm. long, minutely ferruginous-tomentulose; stipular appendages interpetiolar, numerous, minutely pectinate-flagelliform, very minutely ferruginous-pilosulose at the base; inflorescence subumbellate, simple, bearing 4–12 yellowish flowers, peduncle minutely ferruginous-tomentulose, somewhat shorter than the subtending leaves; pedicels 1.0–1.2 cm. long, somewhat accrescent after maturity, minutely ferruginous-tomentulose; bracts narrowly lanceolate, 0.2–0.5 cm. long; calyx-lobes oblong-elliptic, acute to acuminate, 0.9–1.2 cm. long, somewhat foliaceous, minutely appressed ferruginous-puberulent, the internal squamellae broadly deltoid-dentiform, very minutely erose, minutely puberulent-papillate; corolla salverform, minutely ferruginous-puberulent without, the tube 0.9–1.2 cm. long, about 0.2 cm. in diameter at the base, dilated to about 0.4 cm. at the orifice, epistaminal appendages wholly included, 0.1–0.15 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 0.9–1.0 cm.

long, reflexed or widely spreading; stamens inserted slightly above midway within the corolla-tube, the anthers barely included, very narrowly sagittate, 1.0–1.1 cm. long, glabrous; ovary ovoid, about 0.1 cm. long, glabrous or essentially so; stigma 0.2 cm. long; nectaries more or less concrescent at the base, compressed-oblongoid, truncate or slightly erose at the tips, more or less fleshy, conspicuously surpassing the ovary; follicles unknown.

COLOMBIA: MAGDALENA: occasional in damp, somewhat open places in the forest and clearings near streams, alt. 4500–6000 ft., Las Nubes, Dec. 18, 1898, *H. H. Smith 1656* (DL, MBG, NY, TYPE, S).

**54. *Prestonia parviflora* Benth.** in Benth. & Hook. Gen. Pl. 2: 709. 1876.

*Haemadictyon parviflorum* Benth. Pl. Hartw. 355. 1857.

*Temnadenia parviflora* (Benth.) Miers, Apoc. So. Am. 215. 1878.

Stems relatively slender, densely ferruginous-tomentulose, eventually becoming glabrate; leaves rather broadly elliptic, apex shortly acuminate, base broadly obtuse, 7–13 cm. long, 2.5–6.0 cm. broad, firmly membranaceous, above rather sparsely and minutely hispid-hirtellous, more densely along the midrib and veins, beneath densely and ferruginously sericeous-velutinous; petioles 0.8–1.5 cm. long, densely ferruginous-tomentulose; stipular appendages interpetiolar, numerous, pectinate-flagelliform, minutely pilosulose below; inflorescence corymbose to thyrsiform, repeatedly dichotomous, bearing many small, yellowish flowers; peduncle minutely ferruginous-tomentulose, somewhat shorter than the subtending leaves; pedicels 0.4–0.6 cm. long, somewhat accrescent after maturity, minutely ferruginous-tomentulose; bracts minutely linear-lanceolate, 0.1–0.3 cm. long; calyx-lobes ovate-lanceolate, acuminate, 0.3–0.4 cm. long, densely and minutely ferruginous-puberulent, the internal squamellae dentiform, minutely pectinate; corolla salverform, minutely and appressed ferruginous-villosulose without, the tube 0.5–0.6 cm. long, about 0.1 cm. in diameter at the base, somewhat dilated above the insertion of the stamens, epistaminal appendages wholly included, about

0.1 cm. long, faucal annulus conspicuously thickened, the lobes obliquely obovate, very shortly acuminate, 0.6–0.7 cm. long, reflexed or widely spreading; stamens inserted about midway within the corolla-tube, the anthers slightly exserted, sagittate, 0.35 cm. long, glabrous; ovary ovoid, about 0.1 cm. long, minutely papillate; stigma 0.05 cm. long; nectaries imperfectly conerescent, rather thin, somewhat shorter than the ovary; follicles unknown.

COLOMBIA: CUNDINAMARCA: Pandi, date lacking, *Hartweg 1053* (Camb., K, TYPE); Cena, Prov. de Bogota, alt. 1300 m., 1851–57, *Triana s.n.* (Bx, MBG, photograph and analytical drawings); DATA INCOMPLETE: *Triana 1979* (B).

**55. *Prestonia mexicana* A. DC.** in DC. Prodr. 8: 429. 1844; K. Sch. in Engl. & Prantl, Nat Pflanzenfam. 4<sup>2</sup>: 188. 1895.

*Haemadictyon Mexicanum* A. DC. loc. cit. 428. 1844.

*Prestonia sericea* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 360. 1844.

*Haemadictyon contortum* Mart. & Gal. loc. cit. 1844.

*Mitozus Mexicanus* (A. DC.) Miers, Apoc. So. Am. 225. 1878.

*Exothostemon sericeum* (Mart. & Gal.) Miers, loc. cit. 241. 1878.

*Exothostemon contortum* (Mart. & Gal.) Miers, loc. cit. 1878.

Stems relatively stout, densely ferruginous-tomentose, eventually becoming glabrate; leaves broadly ovate to oval or obovate-elliptic, apex acute to very abruptly and shortly acuminate, base rounded to obscurely cordate, 7–23 cm. long, 4–15 cm. broad, firmly membranaceous, above ferruginously hispid-hirtellous to scabridulous upon older specimens, beneath densely ferruginous-tomentose; petioles 0.3–0.9 cm. long, ferruginous-tomentulose; stipular appendages intrapetiolar, numerous, pectinate-flagelliform, ferruginous-tomentulose below; inflorescence closely subumbellate, simple, bearing 8–20 yellowish flowers; peduncle much shorter than the subtending leaves, indument as upon the stem; pedicels 0.5–1.0 cm. long, ferruginous-tomentulose; bracts ovate-lanceolate, acuminate, 0.6–1.7 cm. long, foliaceous; calyx-lobes ovate- to oblong-

lanceolate, acute to acuminate, 1.2–2.3 cm. long, foliaceous, appressed-tomentulose, the internal squamellae broadly dentiform, minutely erose to essentially entire; corolla salverform, densely ferruginous-villosulose without, the tube 2.2–3.0 cm. long, about 0.3–0.35 cm. in diameter at the base, epistaminal appendages replaced by linear callous ridges 0.2–0.25 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 1.3–1.5 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers slightly exserted, oblong-sagittate, 0.6–0.8 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, minutely papillate or essentially glabrous; nectaries concrescent, annular, broadly 5-lobed or essentially entire, about equalling or slightly surpassing the ovary; follicles stout and rigid, sharply divaricate, narrowly napiform, 6–12 cm. long, densely and rigidly ferruginous-hispid; seeds 1.0–1.2 cm. long, the pale tawny coma 2.5–3.0 cm. long.

MEXICO: COLIMA: Manzanillo, Dec. 1–31, 1890, *E. Palmer 1028* (B, G); MORELOS: barranca near Cuernavaca, alt. 4700 ft., June 17, 1896, *Pringle 6341* (B, Bx, BB, DL, G, M, MBG, V); same locality, alt. 5000 ft., Nov. 13, 1895, *Pringle 6224* (B, Bx, BB, DL, G, M, MBG, V); VERA CRUZ: Valle de Cordova, Oct. 15, 1865, *Bourgeau 1500* (B, S); Wartenberg, near Tantoyuca, 1858, *Ervendberg 127* (DC); Zacuapan, June, 1916, *Purpus 7665* (MBG); open forests, Zacuapan, 1928, *Purpus 11134* (MBG); OAXACA: Ojitlan, alt. 700 ft., Aug. 31, 1895, *L. C. Smith 661* (G); San Bartolo, Aug., year lacking, *Andrieux 251* (M); DATA INCOMPLETE: *Schiede 488* (F); *Pavon s.n.* (BB); *Andrieux 398* (DC).

GUATEMALA: SANTA ROSA: Naranjo, alt. 1100 m., May, 1893, *Heyde & Lux 4496* (B, BB, M, MBG); DATA INCOMPLETE: *Warszewicz s.n.* (B).

*Haemadictyon Mexicanum* A. DC., based upon a tracing of a plant of Mociño & Sesse, diverges from typical *P. mexicana* only in the absence of the heavy indument characteristic of the latter species. This absence is considered to be an omission rather than a positive indication of glabrisms, since the thick napiform-fusiform follicles illustrated for Mociño & Sesse's plant are only found in a relatively small group of species always bearing a characteristic ferruginous indument. Upon the basis of a wide representation of the Mexican flora, only one species of *Prestonia* with thick follicles is known, *P. mexicana*; consequently *H. Mexicanum* has been placed in synonymy

under it. The peculiar conditions under which the tracings of Mociño & Sesse's plants were prepared would also support the supposition of an accidental omission of the indument.

**56. *Prestonia amanuensis* Woodson, spec. nov.**

Suffruticosa volubilis; ramulis crassiusculis ferrugineo-tomentosis; foliis late ovatis apice abrupte brevissimeque acuminatis basi late obscureque cordatis 6–9 cm. longis 4–7 cm. latis rigide membranaceis supra dense ferrugineo-hispidulis subtus densius ferrugineo-tomentulosus; petiolis 0.2–0.3 cm. longis ut in ramulo vestitis; appendicibus stipulaceis intrapetiolaribus multis minute pectinatis; inflorescentiis dense subumbellatis simplicibus flores gilvos 6–12 gerentibus; pedunculo foliis multo brevior ut in ramulo vestito; pedicellis 0.3–0.5 cm. longis post maturitatem paulo accrescentibus ferrugineo-tomentulosus; bracteis ovato-lanceolatis acuminatis 0.3–0.7 cm. longis foliaceis; calycis laciniis ovato-lanceolatis acuminatis 1.1–1.3 cm. longis foliaceis minute appressequ hirtellis squamellis dentiformibus minute emarginatis erosive; corollae salverformis extus dense appressequ ferrugineo-villosulae tubo 2.0–2.2 cm. longo basi ca. 0.3 cm. diametro metiente intus plicas subquadratas callosas ca. 0.1–0.15 cm. longas pro appendicibus epistaminalibus gerente faucibus callosis lobis oblique obovatis breviter acuminatis 0.8–0.9 cm. longis patentibus; staminibus prope fauces insertis antheris paululo exsertis sagittatis 0.6 cm. longis glabris; ovario ovoideo ca. 0.14 cm. longo glabriusculo; stigmatibus 0.2 cm. longo; nectariis crescentibus annularibus subintegris ovario subaequantibus; folliculis ignotis.

Stems relatively stout, ferruginous-tomentose; leaves broadly ovate, apex abruptly and shortly acuminate, base broadly and obscurely cordate, 6–9 cm. long, 4–7 cm. broad, firmly membranaceous, above densely ferruginous-hispidulous, beneath densely ferruginous-tomentulose; petioles 0.2–0.3 cm. long, indument as upon the stem; stipular appendages intrapetiolar, numerous, minutely pectinate; inflorescence densely subumbellate, simple, bearing 6–12 cream-colored flowers; peduncle much shorter than the subtending leaves, ferrugi-



nous-tomentose; pedicels 0.3–0.5 cm. long, somewhat accrescent after maturity, ferruginous-tomentulose; bracts ovate-lanceolate, acuminate, 0.3–0.7 cm. long, foliaceous; calyx-lobes ovate-lanceolate, acuminate, 1.1–1.3 cm. long, foliaceous, minutely appressed-hirtellous, the internal squamellae dentiform, minutely emarginate or erose; corolla salverform, densely and appressed ferruginous-villosulose without, the tube 2.0–2.2 cm. long, about 0.3 cm. in diameter at the base, epistaminal appendages replaced by callous subquadrate protuberances 0.1–0.15 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 0.8–0.9 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exerted, sagittate, 0.6 cm. long, glabrous; ovary ovoid, about 0.14 cm. long, essentially glabrous; stigma 0.2 cm. long; nectaries concrescent, annular, essentially entire, about equalling the ovary; follicles unknown.

BRITISH HONDURAS: growing over low bushes in open places, rare, Stann Creek Railway, alt. 50 ft., Aug. 29, 1929, *Schipp* 87 (B, TYPE, G, MBG, photograph and analytical drawings).

Similar to *P. mexicana*, to which it is doubtless closely related, but differing in its smaller, more shortly petiolate leaves, smaller flowers, and particularly in the shape and size of the epistaminal protuberances of the corolla as indicated in the key to species.

**57. *Prestonia isthmica*** Woodson, Ann. Mo. Bot. Gard. 18: 555. 1931.

*Prestonia longituba* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 188. 1895, nom. subnud.

Stems relatively stout, rather finely ferruginous-tomentulose to glabrate, conspicuously lenticellate when fully mature; leaves broadly obovate to oblong-elliptic, apex abruptly and shortly acuminate, base obtuse or rounded, rather obscurely cordate, 9–22 cm. long, 5–13 cm. broad, firmly membranaceous, above rather minutely and sparsely hirtellous-strigillose, beneath minutely ferruginous-tomentulose; petioles 0.3–1.2 cm.

long, indument as upon the stem; stipular appendages intra-petiole, rather broadly pectinate; inflorescence densely sub-umbellate, simple, bearing 4-12 yellowish flowers; peduncle much shorter than the subtending leaves, indument as upon the stem; pedicels 0.5-1.0 cm. long, somewhat accrescent after maturity, minutely ferruginous-tomentulose-papillate; bracts ovate-lanceolate, 0.7-1.2 cm. long, foliaceous; calyx-lobes ovate to ovate-lanceolate, acuminate, 2.0-2.5 cm. long, foliaceous, minutely and rather irregularly hirtellous-papillate without, the internal squamellae broadly dentiform-ligular, minutely erose or lacerate, pilosulose; corolla salverform, ferruginous-villosulose without, the tube 2.5-3.5 cm. long, about 0.3-0.4 cm. in diameter at the base, epistaminal appendages replaced by callous linear ridges 0.2-0.25 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 1.3-1.7 cm. long, reflexed or widely spreading; stamens inserted at about the upper  $\frac{1}{4}$  of the corolla-tube, the anthers oblong-sagittate, 0.6-0.8 cm. long, glabrous; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.15-0.2 cm. long; nectaries concrescent, tubular, deeply 5-lobed, fleshy, conspicuously surpassing the ovary; follicles stout and rigid, narrowly napiform, sharply divaricate, 7-12 cm. long, densely and rigidly ferruginous-hispid; seeds 1.0-1.6 cm. long, the bright tawny coma 3.5-4.5 cm. long.

COSTA RICA: GUANACASTE: collines de Nicoya, May, 1900, *Tonduz 13945* (B); ALAJUELA: buissons, haies, aux collines de Santiago près S. Ramon, May 31, 1901, *Brenes 14376* (B, G); buissons au bord du Tiliri à la Verbena, près Alajuelita, Aug., 1894, *Tonduz 8904* (Bx); SAN JOSE: wet thicket, between Aserri and Tarbaca, alt. 1200-1700 m., Dec. 6, 1925, *Standley 41332* (US, TYPE, MBG, photograph and analytical drawings); Rio Virilla, alt. 1160 m., Oct., 1898, *Tonduz 7441* (B, BB); Rio Virilla près de San Juan, Oct., 1898, *Tonduz 12711* (BB, M, V); S. Jose, date lacking, *Hoffmann 522* (B); PUNTARENAS: forêts du R. Ceibo, près Buenos Aires, alt. 200 m., Febr., 1892, *Pittier 6652* (Bx).

**58. *Prestonia speciosa* Donn. Sm. Bot. Gaz. 27: 435. 1899.**

Stems relatively stout, ferruginous-tomentose, eventually becoming glabrate; leaves ovate to ovate-elliptic, apex abruptly and shortly acuminate, base broadly obtuse or rounded, 10-17 cm. long, 7-11 cm. broad, firmly membranaceous, above rather

sparsely and minutely hispidulous-strigillose generally, densely ferruginous-tomentulose upon the midrib and veins, beneath finely and minutely ferruginous-tomentulose generally; petioles 0.5–1.2 cm. long, densely ferruginous-tomentulose; stipular appendages interpetiolar, numerous, pectinate-flagelliform; inflorescence subumbellate, simple, bearing 4–8 bright yellow flowers; peduncle scarcely surpassing the subtending petioles, or slightly shorter, ferruginous-tomentulose; pedicels 1.0–1.5 cm. long, somewhat accrescent after maturity, minutely ferruginous-tomentulose; bracts narrowly lanceolate, 0.2–0.5 cm. long, slightly foliaceous; calyx-lobes ovate to ovate-oblong, acute, 1.2–1.5 cm. long, minutely and rather irregularly hirtellous, the internal squamellae broadly dentiform-deltoid, minutely emarginate or erose; corolla infundibuliform, minutely ferruginous-villosulose without, the proper-tube 1.5–1.7 cm. long, about 0.35 cm. in diameter at the base, the throat rather narrowly conical-campanulate, 1.5–1.6 cm. long, about 0.8–0.9 cm. in diameter at the orifice, epistaminal appendages replaced by rather inconspicuous, callous, obtriangular, foveolate protuberances 0.1–0.12 cm. long, fauceal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, shortly acuminate, 2.0–2.5 cm. long, widely spreading; stamens inserted at the base of the corolla-throat, the anthers included, oblong-sagittate, 0.8 cm. long, glabrous; ovary ovoid, about 0.15 cm. long, glabrous or minutely papillate; stigma 0.15 cm. long; nectaries conerescent, annular, rather obscurely and irregularly lobed, fleshy, somewhat surpassing the ovary; follicles unknown.

GUATEMALA: SANTA ROSA: Buena Vista, alt. 1700 m., April, 1893, *Heyde & Lux* 4497 (B, BB, G, US, TYPE, MBG, photograph and analytical drawings).

SALVADOR: LA LIBERTAD: cultivated in the garden of the finca, Puerta de la Laguna, April 27, 1922, *Standley 23673* (G, US).

**59. *Prestonia Riedelii* (Muell.-Arg.) Mgf. in Fedde, Rep. Spec. Nov. 20: 26. 1924.**

*Haemadictyon Riedelii* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 170. 1860.

*Temnadenia Riedelii* (Muell.-Arg.) Miers, Apoc. So. Am. 216. 1878.

*Prestomia Muelleri* Rusby, Mem. Torrey Bot. Club 4: 217. 1895.

*Echites* (?) *Riedelii* (Muell.-Arg.) Malme, Bull. Herb. Boiss. II. 4: 196. 1904.

Stems relatively stout, rather finely ferruginous-tomentose to glabrate; leaves broadly ovate to ovate-elliptic, apex acute to acuminate, base broadly obtuse to rounded, 5–18 cm. long, 3–11 cm. broad, membranaceous, above densely hispidulous-strigillose to essentially glabrate, beneath minutely tomentulose to sparsely and irregularly puberulent or pilosulose; petioles 0.7–4.0 cm. long, indument as upon the stem; stipular appendages intrapetiolar, extremely inconspicuous, pectinate; inflorescence bostrychoid-racemose, simple, relatively lax and elongate, bearing 20–45 brownish-yellow flowers; peduncle somewhat shorter than the subtending leaves, indument as upon the stem; pedicels 1.5–2.0 cm. long, somewhat accrescent after maturity, minutely tomentulose; bracts lanceolate to narrowly ovate-lanceolate, 0.5–3.3 cm. long, foliaceous; calyx-lobes elliptic-lanceolate, acuminate, 0.8–2.0 cm. long, foliaceous, minutely puberulent, the internal squamellae broadly deltoid-dentiform, minutely and irregularly erose to essentially entire; corolla salverform, rather indistinctly and irregularly puberulent without, the tube 1.3–1.5 cm. long, about 0.25 cm. in diameter at the base, epistaminal appendages replaced by callous, linear ridges 0.15–0.3 cm. long, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely oblong-elliptic to obovate, 1.1–1.7 cm. long, reflexed or widely spreading; stamens inserted at slightly below midway within the corolla-tube, the anthers wholly included, narrowly oblong-sagittate, shortly auriculate, 0.55–0.65 cm. long, sparsely pilosulose; ovary ovoid, 0.1–0.125 cm. long, minutely papillate; stigma 0.125–0.15 cm. long; nectaries separate or essentially so, compressed-obovoid or oblong-obovoid, about as long as the ovary; follicles relatively elongate and slender, somewhat articulated, usually more or less falcate, occasionally persistently

united at the tips until maturity, 10–25 cm. long, minutely and densely hispidulous; seeds 1.1–1.3 cm. long, obsoletely rostrate, the pale tawny coma about 2.5 cm. long.

PERU: AYACUCHO: Aina, between Huanta and Rio Apurimac, open woods, alt. 750–1000 m., May 7–17, 1929, *Killip & Smith 22708* (US).

BOLIVIA: LA PAZ: Milluhuaya, alt. 1300 m., Dec., 1917, *Buchtien 277* (MBG); Polo-Polo bei Coroico, alt. 1100 m., Oct.–Nov., 1912, *Buchtien 279* (B, DL, MBG); “Yungas,” 1890, *Bong 403* (B, BB, DL, G, M, MBG); TARIJA: Soledad bei S. Luis, Wald, alt. 1500 m., Jan. 30, 1904, *Fiebrig 2675* (B, DL, M, U, V); SANTA CRUZ: Cuesta Negra, alt. 1200 m., Dec. 23, 1921, *Steinbach 6065* (B); Samaipata, Valleggrande, alt. 1200 m., March 10, 1920, *Steinbach 3732* (B); im Wald der Quebrada de Charagua, Dec., 1910, *Herzog 11230* (B, DL).

PARAGUAY: in regione fl. Alto Parana, 1909–10, *Fiebrig 5947* (B); in reg. collum “Cerro de Tobaty,” Sept., 1900, *Hassler 6424* (B, V); in reg. lacus Ypacaray, April, 1913, *Hassler 12166* (C, MBG); ad ripam Piribibuey, Aug., year lacking, *Hassler 3211* (B, V); in altaplanitie et declivibus “Sierra de Amambay,” Dec., 1907, *Bojas 9763a* (B); Cordillera de Altos, Aug., 1902, *Fiebrig 64* (B, DL, M); zwischen Rio Apa und Rio Aquidaban, San Luis, Dec., 1908, *Fiebrig 4447* (B, G, M); in reg. collum, Cordillera de Villa-Rica, Jan., 1905, *Hassler 8678* (B).

BRAZIL: SÃO PAULO: campinas, date lacking, *Novae 11207* (B); Canna Velha, April, 1848, *Regnell III 884* (S); data incomplete, *De Jonghe s.n.* (Camb.); PARANA: ad marginem silvulae, Jaguarahyva, alt. 740 m., April 15, 1911, *Dusen 11624* (MBG, S); ad marginem silvulae, Itarare opp., alt. 730 m., Jan. 21, 1915, *Dusen 16454* (MBG, S, US); Villa Velha, in campo, Febr. 4, 1905, *Dusen 7699* (S).

ARGENTINA: MISIONES: Posadas, La Granja, Dec. 3, 1907, *Ekman 1592* (S).

This is a relatively uniform species. It departs from other representatives of § *Tomentosae* in the relatively scant indument of the corolla. The color of the corolla is reported by Herzog as “rot-braun mit gelbem schlund.”

## 60. *Prestonia Schumanniana* Woodson, spec. nov.

Suffruticosa volubilis; ramulis gracilibus minute ferrugineo-tomentulosis; foliis late ellipticis apice abrupte breviterque acuminatis basi obtusis 12–15 cm. longis 5–8 cm. latis rigide membranaceis supra sparse minutissimeque strigilloso-papillatis nervo medio nervisque minute ferrugineo-pilosulis subtus minutissime ferrugineo-tomentulosis; petiolis 1.1–1.5 cm. longis minutissime tomentulosis; appendicibus stipulaceis interpetiolaribus multis minute pectinatis; inflorescentiis subumbellatis simplicibus vel obscure dichotomis flores 6–12 luteos

gerentibus; pedunculo petiolis subaequante minute ferrugineo-tomentuloso; pedicellis 1.0–1.1 cm. longis post maturitatem paulo accrescentibus minutissime tomentulosis; bracteis ovatis 0.1–0.3 cm. longis; calycis laciniis oblongo-ellipticis apice acutis 0.9–1.1 cm. longis foliaceis minute hirtello-papillatis squamellis late dentiformibus minute emarginatis puberulis; corollae salverformis extus minute ferrugineo-villosulae tubo 1.5 cm. longo basi ca. 0.2 cm. diametro metiente intus plicas callosas minutas late oblongas pro appendicibus epistaminalibus gerente annulo faucium conspicue incrassato tumido lobis oblique obovatis brevissime acuminatis 1.0–1.2 cm. longis patentibus; antheris paululo exsertis elliptico-sagittatis 0.7 cm. longis glabris; ovario ovoideo ca. 0.2 cm. longo glabro; stigmate 0.2 cm. longo; nectariis basi conerescentibus carnis ovarium paulo superantibus; folliculis ignotis.

Stems relatively slender, minutely ferruginous-tomentulose; leaves broadly elliptic, apex abruptly and shortly acuminate, base obtuse, 12–15 cm. long, 5–8 cm. broad, firmly membranaceous, above sparsely and very minutely strigillose-papillate generally, the midrib and nerves minutely ferruginous-pilose, beneath very minutely ferruginous-tomentulose; petioles 1.1–1.5 cm. long, very minutely tomentulose; stipular appendages interpetiolar, numerous, minutely pectinate; inflorescence subumbellate, congested, simple, or obscurely dichotomous, bearing 6–12 yellowish flowers; peduncle about as long as the subtending petioles, minutely ferruginous-tomentulose; pedicels 1.0–1.1 cm. long, slightly accrescent after maturity, very minutely tomentulose; bracts ovate, 0.1–0.3 cm. long; calyxlobes oblong-elliptic, acute, 0.9–1.1 cm. long, foliaceous, minutely hirtellous-papillate, the internal squamellae broadly dentiform, minutely emarginate, puberulous; corolla salverform, minutely ferruginous-villosulose without, the tube 1.5 cm. long, about 0.2 cm. in diameter at the base, epistaminal appendages replaced by broadly oblong, callous ridges, faucal annulus conspicuously thickened or tuberculate, the lobes obliquely obovate, very shortly acuminate, 1.0–1.2 cm. long, re-

flexed or widely spreading; stamens inserted slightly above midway within the corolla-tube, the anthers barely exerted, elliptic-sagittate, 0.7 cm. long, glabrous; ovary ovoid, about 0.2 cm. long, glabrous; stigma 0.2 cm. long; nectaries concrescent at the base, fleshy, somewhat surpassing the ovary; follicles unknown.

ECUADOR: GUAYAS: Balao, May, 1892, *Eggers 14732* (M, TYPE, MBG, photograph and analytical drawings).

Important features of morphology distinguish this species from *P. Riedelii*, the only other representative of § *Tomentosae* in South America with the epistaminal appendages replaced by callous ridges. These may be summarized as follows:

	<i>P. Riedelii</i>	<i>P. Schumanniana</i>
Inflorescence:	simple, lax and elongate.	simple or obscurely dichotomous, congested, subumbellate.
Anthers:	included, pilose, auricles very short.	barely exerted, glabrous, auricles long and slender.
Epistaminal ridges:	linear.	broadly oblong.

#### EXCLUDED OR UNCERTAIN SPECIES

*Prestonia Goudotiana* Baill. Bull. Mens. Soc. Linn. Paris 1: 792. 1889, nom. subnud. Possibly refers to a species of § *Tomentosae*. The nectaries are briefly described, without citation of specimens or other characters by means of which interpretation can be based.

*Prestonia hirsuta* (R. & P.) Spreng. Syst. 1: 637. 1825, not Muell.-Arg. (*Echites hirsuta* R. & P. Fl. Peruv. 2: 19. pl. 136. 1799, not A. Rich.) = *Mandevilla Pavonii* (A. DC.) Woodson, Ann. Mo. Bot. Gard. 19: 73. 1932 (*Echites Pavonii* A. DC. in DC. Prodr. 8: 463. 1844).

*Prestonia Langlassei* Standl. Contr. U. S. Nat. Herb. 23: 1159. 1924 = *Laubertia Pringlei* (Greenm.) Woodson, Ann. Mo.

Bot. Gard. 18: 555. 1931 (*Streptotrachelus Pringlei* Greenm. Proc. Am. Acad. 32: 298. 1897).

*Prestonia peruviana* Spreng. loc. cit. 1825 = **Mandevilla glandulosa** (R. & P.) Woodson, loc. cit. 66. 1932 (*Echites glandulosa* R. & P. loc. cit. pl. 135. 1799).

*Haemadictyon bracteosum* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 168. 1860. I have not been able to examine the type specimen of this species, collected by Riedel near Rio de Janeiro. The description accords with that of *Prestonia perplexa* Woodson (*vide ante*) in all essential characters save the elaborate bracts, which the specific adjective commemorates. In view of that fact, it appears wise to maintain the entities separate.

## XXVII. RHODOCALYX Muell.-Arg.

**Rhodocalyx** Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 172. 1860; Miers, Apoc. So. Am. 138. 1878 (as to *Rh. rotundifolius*).

Lactescent, suffrutescent herbs. Stems terete, erect, simple, or branching at the very base. Leaves opposite, petiolate, entire, penninerved, eglandular, the petioles exappendiculate or essentially so. Inflorescence terminal, simply racemose, conspicuously bracteate. Calyx 5-parted, the lobes somewhat unequal, imbricated, cleft nearly to the receptacle, conspicuously foliaceous or subpetaloid, bearing within at the base deeply lacerate, opposite squamellae. Corolla salverform, exappendiculate within, the orifice of the tube conspicuously annulate, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, included, the anthers connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, narrowly sagittate connective; pollen granular. Carpels 2, united at the apex by a common stylar shaft surmounted by the fusiform-capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate. Follicles 2, apocarpous, terete, dehiscing along the ventral suture, containing numerous dry, rostrate, apically comose seeds (according to Muell.-Arg.).



Type species: *Rhodocalyx rotundifolius* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 173. pl. 51. 1860.

1. *Rhodocalyx rotundifolius* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 173. pl. 51. 1860; Miers, Apoc. So. Am. 138. 1878.

*Echites erecta* A. DC. in DC. Prodr. 8: 469. 1844.

Stems erect, simple, or branched at the base, 2.0–4.5 dm. tall, ferruginous-hirtellous; leaves opposite, shortly petiolate, ovate to suborbicular, apex rounded to very shortly and abruptly acuminate, base broadly obtuse to rounded, the uppermost and the lowermost usually much reduced, 5–9 cm. long, 3.0–9.5 cm. broad, firmly membranaceous, above ferruginous-hispidulous, beneath densely ferruginous-tomentulose; petioles 0.3–0.5 cm. long; inflorescence somewhat surpassing the subtending leaves, bearing 3–18 rather showy flowers; peduncle densely ferruginous-hirtellous; pedicels 1–2 cm. long, ferruginous-hirtellous; bracts very conspicuous and laminate, foliaceous to subpetaloid, oblong to ovate-oblong, about equalling to somewhat surpassing the subtended pedicels; calyx-lobes oblong to ovate-oblong, acute to acuminate, 2.0–2.5 cm. long, the margins ciliolate, otherwise essentially glabrous, rather delicately membranaceous, purplish (according to Muell.-Arg.), the squamellae very deeply lacerate; corolla salverform, glabrous without, the tube 2.0 cm. long, about 0.1 cm. in diameter at the base, the orifice conspicuously annulate, the lobes obliquely obovate, 1.2–1.3 cm. long, somewhat reflexed; stamens inserted somewhat above midway within the corolla-tube, the anthers 0.6 cm. long, essentially glabrous dorsally; ovary ovoid, about 0.1 cm. long, essentially glabrous; stigma 0.15 cm. long; nectaries separate, somewhat shorter than the ovary; follicles unseen.

BRAZIL: MINAS GERAES: data incomplete, *Regnell III 885* (S, US); *Glaziou 12951* (US); MATTO GROSSO: campo, Procdencia Caceres, Sept., 1911, *Hoehne 4697* (US); DATA INCOMPLETE: *Riedel s.n.* (G, NY).

Also reported from the Brazilian states of São Paulo, Bahia, and Espiritu Santo by Mueller, who describes the color of the corolla as dark crimson to rose-purple.

## EXCLUDED SPECIES

*Rhodocalyx calycosus* (A. Rich.) Miers, Apoc. So. Am. 140. 1878 (*Echites calycosa* A. Rich. in Sagra, Hist. Cuba 11: 94. 1850) = **Asketanthera calycosa** (A. Rich.) Woodson, Ann. Mo. Bot. Gard. 19: 47. 1932.

*Rhodocalyx cinereus* (A. Rich.) Miers, Apoc. So. Am. 141. 1878 (*Echites cinerea* A. Rich. in Sagra, Hist. Cuba 11: 93. 1850) = **Haplophyton cinereum** (A. Rich.) Woodson, comb. nov. Notes on the relegation of this species will be found on p. 231.

*Rhodocalyx coccineus* (Hook. & Arn.) Miers, Apoc. So. Am. 141. 1878 (*Echites coccinea* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834) = **Mandevilla coccinea** (Hook. & Arn.) Woodson, Ann. Mo. Bot. Gard. 20: 734. 1933.

*Rhodocalyx crassifolius* (Muell.-Arg.) Miers, Apoc. So. Am. 139. 1878 (*Amblyanthera crassifolia* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 143. 1860) = **Galactophora crassifolia** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 50. 1932.

*Rhodocalyx crassipes* (A. Rich.) Miers, Apoc. So. Am. 140. 1878 (*Echites crassipes* A. Rich. in Sagra, Hist. Cuba 11: 91. 1850) = **Echites umbellata** Jacq. var. **crassipes** (A. Rich.) Gomez, Anal. Soc. Espan. Hist. Nat. 23: 274. 1894.

*Rhodocalyx cuneifolius* Miers, Apoc. So. Am. 142. 1878. Perhaps equivalent to *Mandevilla velutina* (Mart.) Woodson.

*Rhodocalyx hypoleucus* (Benth.) Miers, Apoc. So. Am. 140. 1878 (*Echites hypoleuca* Benth. Pl. Hartw. 23. 1839) = **Macrosiphonia hypoleuca** (Benth.) Muell.-Arg. Linnaea 30: 452. 1860.

*Rhodocalyx lanuginosus* (Mart. & Gal.) Miers, Apoc. So. Am. 139. 1878 (*Echites lanuginosa* Mart. & Gal. Bull. Acad. Roy. Brux. 11<sup>1</sup>: 357. 1844) = **Macrosiphonia lanuginosa** (Mart. & Gal.) Hemsl. Biol. Centr.-Am. Bot. 2: 316. 1882.

*Rhodocalyx ovatus* Miers, Apoc. So. Am. 141. 1878 = **Mandevilla coccinea** (Hook. & Arn.) Woodson, Ann. Mo. Bot. Gard. 20: 734. 1933 (*Echites coccinea* Hook. & Arn. in Hook. Jour. Bot. 1: 286. 1834).

*Rhodocalyx suaveolens* (Mart. & Gal.) Miers, Apoc. So. Am. 139. 1878 (*Echites suaveolens* Mart. & Gal. Bull. Acad. Roy.

BRUX. 11<sup>1</sup>: 356. 1844, not A. DC.) = *Macrosiphonia hypoleuca* (Benth.) Muell.-Arg. *Linnaea* 30: 452. 1860 (*Echites hypoleuca* Benth. Pl. Hartw. 23. 1839).

*Rhodocalyx Tweedianus* Miers, Apoc. So. Am. 142. 1878. Probably a species of *Mandevilla*.

## XXVIII. LAUBERTIA A. DC.

*Laubertia* A. DC. in DC. Prodr. 8: 486. 1844; Benth. & Hook. Gen. Pl. 2: 724. 1876; Miers, Apoc. So. Am. 124. 1878; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4<sup>2</sup>: 170. 1895.

*Streptotrachelus* Greenm. Proc. Am. Acad. 32: 298. 1897.

Lactescent, fruticose or suffruticose lianas. Stems volubile, terete; branches alternate or opposite below. Leaves opposite to occasionally ternate or quaternate, petiolate, entire, penninerved, eglandular; petioles somewhat girdling at the nodes, subtended by numerous minute, pectinate, adaxial, stipular appendages. Inflorescence lateral, alternate, occasionally subterminal or terminal, di- or trichotomously scorpioid, bracteate, bearing few to numerous rather mediocre flowers. Calyx 5-parted, the lobes equal to subequal, slightly foliaceous, cleft nearly to the receptacle, imbricated, eglandular within. Corolla salverform, minutely ferruginous-pubescent without, the tube straight or spirally contorted, exappendiculate within, the orifice conspicuously annulate, the limb actinomorphic, 5-parted, dextrorsely convolute. Stamens 5, the anthers somewhat exserted, connivent and agglutinated to the stigma, consisting of 2 parallel, basally protuberant sporangia borne ventrally near the apex of an enlarged, acutely sagittate connective; pollen granular. Carpels 2, connected at the apex by the common stylar shaft surmounted by the fusiform-capitate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or somewhat conercent at the base. Follicles 2, apocarpous, terete, dehiscing along the ventral suture, containing many dry, truncate, apically comose seeds.

Type species: *Laubertia Boissierii* A. DC. in DC. Prodr. 8: 487. 1844.

## KEY TO THE SPECIES

- a. Corolla-tube straight, not spirally contorted; species of South America.
  - b. Inflorescence much surpassing the subtending leaves, conspicuously and usually repeatedly compound; calyx-lobes ovate-trigonal....1. *L. Boissierii*
  - bb. Inflorescence about equalling, or somewhat shorter than the subtending leaves, rather obscurely compound to essentially simple; calyx-lobes oblong-linear.....2. *L. Sanctae-Martae*
- aa. Corolla-tube spirally contorted; species of Mexico and Central America.
  - b. Calyx-lobes ovate-lanceolate, 0.3–0.45 cm. long; corolla-tube 2.0–2.3 cm. long, anther tips exserted.....3. *L. Pringlei*
  - bb. Calyx-lobes narrowly oblong-elliptic, 0.9–1.1 cm. long; corolla-tube 1.3–1.4 cm. long; anthers barely included.....4. *L. peninsularis*

1. *Laubertia Boissierii* A. DC. in DC. Prodr. 8: 487. 1844; Miers, Apoc. So. Am. 124. 1878.

*Echites Eggersii* Mgf. Notizblatt 9: 78. 1924.

Stems relatively stout, finely ferruginous-hirtellous when young, becoming glabrate and conspicuously lenticellate when fully mature; leaves opposite, occasionally ternate or quaternate, petiolate, ovate to oblong-lanceolate, apex acute to acuminate, base broadly obtuse to rounded or obscurely cordate, 4–18 cm. long, 1–9 cm. broad, firmly membranaceous, above minutely hirtellous to glabrate, beneath finely and rather sparsely puberulent when young, eventually glabrate; petioles 1.0–1.5 cm. long, minutely and rather sparsely puberulent to glabrate; inflorescence much surpassing the subtending leaves, scorpioid, the peduncle conspicuously and usually repeatedly compound, bearing relatively numerous, greenish-purple or reddish flowers; pedicels 0.8–1.2 cm. long, finely puberulent-papillate; bracts minutely ovate, scarious to only slightly foliaceous; calyx-lobes ovate-trigonal, sharply acute to acuminate, 2.0–3.5 cm. long, minutely and ferruginously puberulent-papillate without, slightly foliaceous to nearly scarious; corolla salverform, rather indistinctly puberulent-papillate without, the tube 1.5–2.0 cm. long, about 0.25 cm. in diameter at the base, straight, not spirally contorted, the lobes obliquely obovate-dolabriform, 1.0–1.5 cm. long, reflexed; stamens inserted near the orifice of the corolla-tube, the anthers somewhat exserted, 0.6 cm. long, glabrous to minutely puberulent-papillate dorsally; ovary about 0.125 cm. long, glabrous to indefinitely papil-

late; nectaries nearly equalling the ovary; follicles relatively slender, rather obscurely moniliform, 25–40 cm. long, glabrous; seeds 1.0–1.5 cm. long, the pale tawny coma 2.0–2.5 cm. long.

ECUADOR: MANABI: im Wäldern bei El Reereo, April 30, 1897, *Eggers 15681* (B, FM, MBG, NY); DATA INCOMPLETE: *Pavon s.n.* (BB, TYPE, MBG, photograph and analytical drawings).

PERU: SAN MARTIN: on riverside brush, La Merced, alt. 2000 ft., Aug. 10–24, 1923, *Macbride 5473* (FM, US); edge of montaña along trail, Muña, alt. 7000 ft., May 23–June 4, 1923, *Macbride 3902* (FM, US).

2. *Laubertia Sanctae-Martae* (Rusby) Woodson, Ann. Mo. Bot. Gard. 18: 555. 1931.

*Echites Sanctae-Martae* Rusby, Descr. So. Am. Pl. 85. 1920.

Stems relatively slender, minutely ferruginous-puberulent when young, becoming glabrate at maturity; leaves opposite, petiolate, elliptic, apex acuminate, base acutely cuneate, 10–15 cm. long, 1.5–4.5 cm. broad, rather delicately membranaceous, minutely and rather sparsely pilosulose to glabrate above, glabrous beneath; petioles 1.0–1.3 cm. long; inflorescence about equalling, or somewhat shorter than the subtending leaves, rather obscurely, and usually only once dichotomous to essentially simple, bearing several greenish-purple or reddish flowers; pedicels 0.8–1.0 cm. long, minutely and rather sparsely puberulent, greatly accrescent in fruit; bracts minutely lanceolate to linear, 0.1–0.3 cm. long, somewhat foliaceous; calyxlobes oblong-linear, acute to acuminate, 0.4–0.6 cm. long, rather conspicuously foliaceous, minutely and ferruginously appressed-puberulent without; corolla salverform, minutely and ferruginously appressed-puberulent without, the tube straight, not spirally contorted, 2.4–2.7 cm. long, about 0.3 cm. in diameter at the base, the lobes obliquely obovate-dolabriform, 0.9–1.1 cm. long, reflexed; stamens inserted at about the upper  $\frac{1}{3}$  of the corolla-tube, the anthers slightly exserted, 0.55–0.6 cm. long, minutely papillate dorsally; ovary ovoid, about 0.15 cm. long, essentially glabrous; nectaries about equalling the ovary; follicles relatively slender, rather distantly moniliform, 40–45 cm. long, glabrous; seeds 1.0–1.3 cm. long, the pale tawny coma 3.0–3.5 cm. long.

COLOMBIA: MAGDALENA: rare in ravines and on wooded hillsides near Valparaiso, alt. 4000–5000 ft., Jan. 20, 1899, *Smuth 1643* (MBG, NY, TYPE); data incomplete, *Smuth 2525* (MBG, NY).

**3. *Laubertia Pringlei* (Greenm.) Woodson, Ann. Mo. Bot. Gard. 18: 555. 1931.**

*Streptotrachelus Pringlei* Greenm. Proc. Am. Acad. 32: 298. 1897.

*Prestonia Langlassei* Standl. Contr. U. S. Nat. Herb. 23: 1159. 1924.

Stems relatively stout, minutely hirtellous when young, becoming glabrate at maturity; leaves opposite, petiolate, broadly ovate- to oblong-elliptic, apex shortly acuminate, base rounded to very obscurely cordate, 5–10 cm. long, 2.5–5.0 cm. broad, membranaceous, very minutely and rather sparsely puberulent to essentially glabrate above and beneath; petioles 1.5–3.0 cm. long, minutely and rather sparsely puberulent; inflorescence simple or essentially so, about equalling, or somewhat shorter than the subtending leaves, bearing several greenish-purple flowers; pedicels 1.0–1.5 cm. long, minutely and rather sparsely appressed-puberulent; bracts narrowly lanceolate, 0.1–0.3 cm. long, somewhat foliaceous; calyx-lobes ovate-lanceolate, acuminate, 0.3–0.45 cm. long, minutely hirtellous without, somewhat foliaceous; corolla salverform, minutely ferruginous-puberulent without, the tube spirally contorted at about midway below the insertion of the stamens, 2.0–2.3 cm. long, about 0.3 cm. in diameter at the base, the lobes rather broadly dolabriform, 0.7–0.8 cm. long, reflexed; stamens inserted somewhat above midway within the corolla-tube, the anthers 0.7–0.75 cm. long, minutely hirtellous dorsally, the tips slightly exserted; ovary ovoid, about 0.15 cm. long, minutely hirtellous; nectaries somewhat shorter than the ovary; mature follicles unknown, the immature relatively slender, rather distantly moniliform, finely and ferruginously appressed-hirtellous.

MEXICO: MORELOS: lava beds near Cuernavaca, alt. 5200 ft., Sept. 23, 1896, *Pringle 6554* (G, TYPE, MBG); SINALOA: near Colomar, July, 1897, *Rose 1716* (US).

#### 4. *Laubertia peninsularis* Woodson, spec. nov.

Fruticosa volubilis altitudine ignota e fragmento vix facile descripta; ramulis crassiusculis dense ferrugineo-tomentulosis; foliis oppositis petiolatis ovato-ellipticis apice acuminatis basi rotundatis vel obscurissime cordatis 6–13 cm. longis 4–7 cm. latis (fide cl. Schipp) firme membranaceis supra juventate minute puberulis maturitate glabratis subtus minute ferrugineo-puberulis; petiolis 2.0–2.3 cm. longis minute ferrugineo-puberulis; inflorescentiis foliis brevioribus flores mediocres gilvos (fide cl. Schipp) 10–20 gerentibus; pedunculo di- vel trichotomo dense ferrugineo-hirtello; pedicellis congestis 0.8–1.0 cm. longis dense ferrugineo-hirtellis; bracteis anguste lanceolatis 0.2–0.4 cm. longis caducis; calycis laciniis oblongo-ellipticis acutis acuminatisve 0.9–1.1 cm. longis conspicue subfoliaceis extus intusque ferrugineo-hirtellis; corollae salverformis extus minute ferrugineo-hirtellae tubo 1.3–1.4 cm. longo basi ca. 0.25 cm. diametro metiente prope medium paulo contorto lobis oblique obovatis obtusis 0.9–1.1 cm. longis patentibus; antheris 0.5 cm. longis dorso minute puberulo-papillatis apice paulo inclusis; ovario ovoideo ca. 0.15 cm. longo glabro; nectariis ovoideis ovario subaequantibus; folliculis ignotis.

Stems relatively stout, densely ferruginous-tomentulose; leaves opposite, petiolate, ovate-elliptic, apex acuminate, base rounded to very obscurely cordate, 6–13 cm. long, 4–7 cm. broad, firmly membranaceous, above minutely puberulent when young to essentially glabrate at maturity, beneath minutely ferruginous-puberulent; petioles 2.0–2.3 cm. long, minutely ferruginous-puberulent; inflorescence somewhat shorter than the subtending leaves, bearing 10–20 mediocre, cream-colored flowers; peduncle di- or trichotomous, densely ferruginous-hirtellous; pedicels congested toward the upper half of the peduncle, 0.8–1.0 cm. long, ferruginous-hirtellous; bracts narrowly lanceolate, 0.2–0.4 cm. long, caducous; calyx-lobes oblong-elliptic, acute to acuminate, 0.9–1.1 cm. long, conspicuously subfoliaceous, minutely ferruginous-hirtellous within and without; corolla salverform, minutely ferruginous-hirtellous without, the tube 1.3–1.4 cm. long, about 0.25 cm. in di-

anther at the base, spirally contorted at above midway immediately below the insertion of the stamens, the lobes obliquely obovate, obtuse, 0.9–1.1 cm. long, reflexed; stamens inserted at about midway within the corolla-tube, the anthers barely included, 0.5 cm. long, minutely puberulent-papillate dorsally; ovary ovoid, about 0.15 cm. long, essentially glabrous; nectaries ovoid, somewhat shorter than the ovary; follicles unknown.

BRITISH HONDURAS: B. H.-Guatemala Boundary Survey, spring or summer, 1934, *Schipp s.n.* (MBG, TYPE).

In the spring of 1934, when Schipp accompanied an expedition to determine the boundary between Guatemala and British Honduras, he carried vials containing alcoholic preservative for apocynaceous flowers intended for me. While on this trip Mr. Schipp collected a number of interesting novelties, including the type of *Odontadenia Schippii* Woodson, the only known representative of the genus north of Panama. Unfortunately, however, herbarium specimens of several Apocynaceae were completely spoiled in transit, with the survival only of the alcoholic specimens intended primarily for anatomical studies. Such circumstances befell the collections of *Laubertia peninsularis*. Nevertheless, the preserved specimen was ample to show the plant to be a new species of this poorly understood genus, and a fragment of it is now incorporated in the herbarium of the Missouri Botanical Garden. Mr. Schipp describes his plant as "a tall vine growing in dense forest shade, the leaves of which are about five inches long and two and one-half wide. Flowers cream and slightly perfumed."

#### EXCLUDED SPECIES

*Laubertia* (?) *laxiflora* Rusby, Bull. N. Y. Bot. Gard. 4: 408. 1907 = *Odontadenia laxiflora* (Rusby) Woodson, Ann. Mo. Bot. Gard. 19: 386. 1932.

#### CORRIGENDA

Page references are to the parenthetical numbers at the bottom of the pages of "Studies in the Apocynaceae. IV." Pages



1-186 are contained in Ann. Mo. Bot. Gard. 20; 187-340 in 22; and 341-563 in 23.

- p. 101. Remove *Echites obovata* Nees from synonymy.
- p. 105. **Mandevilla pulchra** Woodson, nom. nov.  
*Dipladenia glabra* Rusby, Descr. So. Am. Pl. 88. 1920.  
*Mandevilla glabra* (Rusby) Woodson, Ann. Mo. Bot. Gard. 20: 709. 1933, not N. E. Br.
- p. 128. **Mandevilla velutina** (Mart.) Woodson, var. **angustifolia** (Stadelm.) Woodson, comb. nov.  
*Echites Pohliana* Stadelm. var.  $\alpha$  *angustifolia* Stadelm. Flora 24<sup>1</sup>: Beibl. 73. 1841.  
*Dipladenia gentianoides* Muell.-Arg.  $\beta$  *glabra* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 124. pl. 37. fig. 2. 1860.  
*Mandevilla velutina* (Mart.) Woodson, var. *glabra* (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 20: 732. 1933.
- p. 183. **Macrosiphonia petraea** (St. Hil.) K. Sch. var. **minor** (Hook.) Woodson, comb. nov.  
*Echites grandiflora* Desf. var. *minor* Hook. Jour. Bot. 1: 286. 1834.  
*Macrosiphonia verticillata* Muell.-Arg.  $\delta$  *pinifolia* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 141. 1860.  
*Macrosiphonia petraea* (St. Hil.) K. Sch. var. *pinifolia* (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 20: 787. 1933.
- p. 266. In place of *Angadenia Lindeniana* (Muell.-Arg.) Miers read:  
**Angadenia Berterii** (A. DC.) Miers, Apoc. So. Am. 180. 1878 (*Echites Berterii* A. DC. in DC. Prodr. 8: 447. 1844).

#### ADDENDA

Page references are to the parenthetical numbers at the bottom of the pages of "Studies in the Apocynaceae. IV." Pages 1-186 are contained in Ann. Mo. Bot. Gard. 20; 187-340 in 22; and 341-563 in 23.

## II. MESECHITES Muell.-Arg.

- p. 26. To synonymy of *M. trifida* (Jacq.) Muell.-Arg., add:  
*Echites chlorantha* Schlecht. *Linnaea* 26: 663. 1853;  
 Miers, *Apoc. So. Am.* 196. 1878.
- p. 36. To synonymy of *M. angustifolia* (Poir.) Miers, add:  
*Echites concolor* Ham. *Prodr.* 31. 1825.

## III. MANDEVILLA Lindl.

- p. 99. To synonymy of *M. Martiana* (Stadelm.) Woodson, var.  
*glabra* (Muell.-Arg.) Woodson, add:  
*Micradenia acuminata* (Hook.) Miers, *Apoc. So. Am.*  
 162. 1878.  
 To synonymy of *M. crassinoda* (Gardn.) Woodson, add:  
*Micradenia nodulosa* Miers, *Apoc. So. Am.* 159. 1878.
- p. 120. To synonymy of *M. atrovioleacea* (Stadelm.) Woodson,  
 add:  
*Micradenia atrovioleacea* (Stadelm.) Miers, var. *ovata*  
 Miers, *Apoc. So. Am.* 159. 1878.
- p. 124. To synonymy of *M. illustris* (Vell.) Woodson, var.  
*typica*, add:  
*Echites Gardneriana* A. DC. in DC. *Prodr.* 8: 483.  
 1844.  
*Echites Gardneriana* A. DC.  $\beta$  *grandiflora* A. DC. loc.  
 cit. 1844.
- p. 128. To synonymy of *M. velutina* (Mart.) Woodson, var.  
*angustifolia* (Stadelm.) Woodson, comb. nov., add:  
*Dipladenia longiloba* A. DC. in DC. *Prodr.* 8: 485.  
 1844; Miers, *Apoc. So. Am.* 157. 1878.
- p. 130. To synonymy of *M. coccinea* (Hook. & Arn.) Woodson,  
 add:  
*Dipladenia ? coccinea* (Hook. & Arn.) Muell.-Arg. in  
 Mart. *Fl. Bras.* 6<sup>1</sup>: 132. 1860.
- p. 135. To synonymy of *M. subspicata* (Vahl) Mgf., add:  
*Laseguea latiuscula* Miers, *Apoc. So. Am.* 251. 1878.
- p. 148. To synonymy of *M. scabra* (R. & S.) K. Sch., add:  
*Echites canescens* Willd. ex R. & S. *Syst.* 4: 795. 1819.

- Echites bicolor* Miq. Stirp. Surinam. Select. 154. 1851.  
*Laseguea bicolor* (Miq.) Miers, Apoc. So. Am. 251. 1878.
- p. 152. To synonymy of **M. leptophylla** (A. DC.) K. Sch., add:  
*Amblyanthera leptophylla* (A. DC.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 142. 1860.
- p. 154. To synonymy of **M. Fendleri** (Muell.-Arg.) Woodson, add:  
*Mitozus discolor* Miers, Apoc. So. Am. 224. 1878.  
*Echites discolor* Moritz, ex Miers, loc. cit. nom. nud. in synon.
- p. 173. To the excluded species of *Mandevilla*, add:  
*Mandevilla crassifolia* (Spruce) K. Sch. ex Mg. in Fedde, Rep. Sp. Nov. 20: 24. 1924, sphalm. = **Galactophora crassifolia** (Muell.-Arg.) Woodson, Ann. Mo. Bot. Gard. 19: 50. 1923 (*Amblyanthera crassifolia* Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 143. 1860).  
*Mandevilla Wrightiana* (Muell.-Arg.) Benth. & Hook. Gen. Pl. 2: 727. 1876 (*Rhabdadenia Wrightiana* Muell.-Arg. Linnaea 30: 438. 1860) = **Neobracea Valenzuelana** (A. Rich.) Urb. Symb. Ant. 9: 241. 1924 (*Echites Valenzuelana* A. Rich. in Sagra, Hist. Cub. 11: 93. 1850).

To the recognized species of *Mandevilla* add the following:

**Mandevilla Pittieri** Woodson, spec. nov.

Suffrutescens e rhizomate subtuberoso volubilis; ramis gracilibus ca. 4.5–6.0 dm. altis glaberrimis; foliis oppositis petiolatis oblongo-ellipticis apice breviter acuminatis basi late obtusis rotundatisve 7–8 cm. longis 3.0–3.5 cm. latis firmiter membranaceis glaberrimis supra sublutescentibus nervo medio basi pauciglanduligero subtus opacis; petiolis 1.2–1.5 cm. longis glabris; appendicibus stipulaceis minutissimis vix bene visis; racemis simplicibus terminalibus subterminalibusve flores 3–5 gilvos (?) speciosos gerentibus; pedunculo petiolos ca. bis superante glabro; pedicellis 2 cm. longis glaberrimis; bracteis

haud visis; calycis laciniis ovatis acuminatis 0.45–0.5 cm. longis extus minutissime papillatis squamellis multis; corollae infundibuliformis extus omnino glabrae tubo proprio 1.3 cm. longo ca. 0.18 cm. basi diametro metiente faucibus anguste conicis 1.4 cm. longis ostio ca. 0.7 cm. diametro metiente lobis oblique obovatis 1.6–1.7 cm. longis patulis; antheris 0.9 cm. longis glabris; ovario oblongoideo in stylo gradatim angustato ca. 0.3 cm. longo glabro; stigmatum umbraculiforme breviter obtuseque apiculato 0.35 cm. longo; nectariis 2 manifeste inaequalibus ovario multo brevioribus; folliculis ignotis.

Suffrutescent; rhizome subtuberosus; stems relatively slender, glabrous, 4.5–6.0 cm. tall, somewhat twining at the tips; leaves opposite, petiolate, oblong-elliptic, apex shortly (somewhat subcaudate-) acuminate, base broadly obtuse to rounded, 7–8 cm. long, 3.0–3.5 cm. broad, firmly membranaceous, glabrous, somewhat lustrous above, glandular at the base of the midrib, opaque beneath; petioles 1.2–1.5 cm. long, glabrous; stipular appendages extremely minute, scarcely visible; racemes simple, terminal or subterminal, bearing 3–5 showy, creamy white flowers; peduncle about twice surpassing the subtending petioles, glabrous; pedicels 2 cm. long, glabrous; bracts not seen; calyx-lobes ovate, acuminate, 0.45–0.5 cm. long, very minutely papillate without, the squamellae numerous, indefinitely distributed; corolla infundibuliform, glabrous without, the proper tube 1.3 cm. long, about 0.18 cm. in diameter at the base, the throat narrowly conical, 1.4 cm. long, about 0.7 cm. in diameter at the orifice, the lobes obliquely obovate, 1.6–1.7 cm. long, spreading; anthers 0.9 cm. long, glabrous; ovary oblongoid, about 0.3 cm. long, glabrous; stigma umbraculiform, shortly and obtusely apiculate, 0.35 cm. long, nectaries 2, manifestly unequal, much shorter than the ovary; follicles unknown.

COSTA RICA: forêts de Luis, alt. 650 m., Nov., 1897, Pittier 11551 (B, TYPE, MBG, photograph and analytical drawings).

This is the only species of the *Dipladenia* plexus of *Mandevilla* known from north of Colombia. Its most pronounced affinities appear to be with *M. cereola* Woods., of Ecuador and Bolivia, from which it may be distinguished by its foliar glands

at the base of the midrib above, slight tendency to twine, and narrower corolla throat.

***Mandevilla collium* Woodson, spec. nov.**

Fruticosa volubilis altitudine ignota; ramulis gracilibus glaberrimis maturitate bene lenticellatis; foliis oppositis petiolatis obovatis apice brevissime acuminatis basi late obscurissimeque cordatis 5–8 cm. longis 3.0–4.5 cm. latis membranaceis supra nervo medio basi pauciglandulifero ibique molliter puberulo caeterumque glabris glabratissime subtus nervo medio basi puberulis caeterumque glabris; petiolis 1–2 cm. longis molliter puberulis; appendicibus stipulaceis interpetiolaribus conspicuis maturitate coriaceis unguiformibus; racemis simplicibus lateralibus; pedunculo ca. 7 cm. longo glaberrimo prope apicem flores gilvos (?) speciosos 5–7 gerente; pedicellis 0.5–0.7 cm. longis glabris; bracteis caducis haud visis; calycis laciniis ovatis longe acuminatis 0.6 cm. longis squamellis multis; corollae infundibuliformis extus glabrae tubo proprio 1.0–1.1 cm. longo ca. 0.2 cm. basi diametro metiente faucibus anguste conicis 2.0–2.2 cm. longis ostio ca. 0.65 cm. diametro metiente lobis oblique obovatis breviter acutis 2.0–2.2 cm. longis patulis; antheris oblongo-sagittatis 0.6 cm. longis glabris; ovariis oblongoideis ca. 0.1 cm. longis glabris; stigmatibus umbraculiforme breviter obtuseque apiculato ca. 0.3 cm. longo; nectariis 2 valde inaequalibus ovarium ca. dimidio aequantibus; folliculis ignotis.

Fruticose lianas; stems relatively slender, glabrous, conspicuously lenticellate when fully mature; leaves opposite, petiolate, obovate, apex very shortly acuminate, base broadly and very obscurely cordate, 5–8 cm. long, 3.0–4.5 cm. broad, membranaceous, above inconspicuously glandular at the base of the midrib, where softly puberulent as well, otherwise glabrous, beneath softly puberulent toward the base of the midrib and otherwise glabrous; petioles 1–2 cm. long, softly puberulent; stipular appendages interpetiolar, conspicuous, coriaceous and unguiform at maturity; racemes simple, lateral; peduncle about 7 cm. long, glabrous, bearing 5–7 creamy-white flowers toward the tip; pedicels 0.5–0.7 cm. long, glabrous;

bracts caducous, not seen; calyx-lobes ovate, narrowly acuminate, 0.6 cm. long, glabrous, squamellae numerous, indefinitely distributed; corolla infundibuliform, glabrous without, the proper tube 1.0–1.1 cm. long, about 0.2 cm. in diameter at the base, the throat narrowly conical, 2.0–2.2 cm. long, about 0.65 cm. in diameter at the orifice, the lobes obliquely obovate, shortly acute, 2.0–2.2 cm. long, spreading; anthers oblong-sagittate, 0.6 cm. long, glabrous; ovary oblongoid, about 0.1 cm. long, glabrous; stigma umbraculiform, shortly and bluntly apiculate, about 0.3 cm. long; nectaries 2, manifestly unequal, about half equalling the ovary; follicles unknown.

BOLIVIA: LA PAZ: Trockenbusch, Conzata, alt. 1300 m., Sept. 20, 1926, *Troll 2687* (B, TYPE, MBG, photograph and analytical drawing).

Closely related to *M. oblongifolia* Woods. and *M. pulchra* Woods., also indigenous to Bolivia, from which it may be distinguished as follows:

- Leaves generally puberulent throughout; corolla throat broadly conical, about 1.5 cm. in diameter at the orifice; squamellae in alternate groups of 4–8  
 ..... *M. oblongifolia*
- Leaves glabrous throughout, or essentially so.
- Leaves inconspicuously puberulent toward the base of the midrib; corolla throat narrowly conical, about 0.65 cm. in diameter at the orifice; squamellae numerous, indefinitely distributed..... *M. collum*
- Leaves glabrous throughout; corolla throat rather narrowly conical, 0.8–1.0 cm. in diameter at the orifice; squamellae in alternate groups of 2–4  
 ..... *M. pulchra*

**Mandevilla Krukovii** Woodson, spec. nov.

Fruticosa volubilis; ramulis graciliusculis teretibus sparse pilosulis glabratissve; foliis oppositis breviter petiolatis oblongo-oblancoatis apice breviter acuminatis basi obscure auriculatis 8–12 cm. longis 3–4 cm. latis firme membranaceis supra nervo medio sparse pilosulo ibique sparse glanduligero caeterumque glabris subtus sparse ferrugineo-pilosulis; petiolis 0.7–1.0 cm. longis pilosulis; inflorescentiis simplice racemosis alterno-lateralibus; pedunculo foliis subaequante minutissime pilosulo; pedicellis 0.2–0.3 cm. longis similiter vestitis; bracteis magnis late ovatis conspicue caudatis 2.0–2.8 cm. longis membranaceis planis petaloideis minutissime puberulis

caducis; calycis laciniis ovato-lanceolatis acuminatis 0.7–0.8 cm. longis minutissime puberulis squamellis oppositis irregulariter erosis; corollae infundibuliformis (colore luteo-aurantiacae ?) extus dense minutissime appresse-puberulae tubo proprio cylindrico 3.2–3.5 cm. longo basi ca. 0.3 cm. diametro metiente faucibus tubulo-conicis 0.9–1.0 cm. longis ostio ca. 0.6 cm. diametro metiente lobis oblique obovatis breviter acuminatis 1.7–1.8 cm. longis patulis; antheris latiuscule oblongo-ob lanceolatis apice obtusiusculis basi brevissime auriculatis ca. 0.5 cm. longis glabris; ovario oblongoideo ca. 0.125 cm. longo glabro; stigmatе umbraculiforme breviter apiculato ca. 0.15 cm. longo; nectariis 5, compresse obovoideis ovario paulo brevioribus; folliculis crassiusculis conspicue moniliformibus 25–28 cm. longis minute puberulis; seminibus 1.2 cm. longis como aurantiaco ca. 2 cm. longo.

Fruticose lianas; branches relatively slender, terete, sparsely pilosulose to glabrate; leaves opposite, shortly petiolate, oblong-ob lanceolate, apex shortly acuminate, base obscurely auriculate, 8–12 cm. long, 3–4 cm. broad, firmly membranaceous above, sparsely pilosulose and glandular along the midrib, otherwise essentially glabrous, beneath sparsely and generally ferruginous-pilosulose; petioles 0.7–1.0 cm. long, pilosulose; inflorescence simply racemose, alternate-lateral, bearing 20–25 showy, yellowish-orange (?) flowers; peduncle about equalling the subtending leaves, very minutely pilosulose; pedicels 0.2–0.3 cm. long, minutely pilosulose; bracts showy, petalaceous, membranaceous, broadly ovate, conspicuously caudate, 2.0–2.8 cm. long, very minutely puberulent, caducous; calyx-lobes ovate-lanceolate, acuminate, 0.7–0.8 cm. long, very minutely puberulent, the opposite squamellae irregularly erose; corolla infundibuliform, slightly gibbous, the proper-tube cylindrical, 3.2–3.5 cm. long, about 0.3 cm. in diameter at the base, the throat tubular-conical, 0.9–1.0 cm. long, about 0.6 cm. in diameter at the orifice, the lobes obliquely obovate, shortly acuminate, 1.7–1.8 cm. long, patulous; anthers rather broadly oblong-ob lanceolate, apex obtusish, base very shortly auriculate, about 0.5 cm. long, glabrous; ovaries oblongoid, gradually narrowed

to the style, about 0.125 cm. long, glabrous; stigma umbraculiform, shortly apiculate, about 0.15 cm. long; nectaries 5, compressed-obovoid, somewhat shorter than the ovary; follicles rather stout, conspicuously moniliform, 25–28 cm. long, minutely puberulent; seeds 1.2 cm. long, the bright orange coma about 2 cm. long.

BRAZIL: AMAZONAS: Municipality Humayta, near Tres Casas, on low terra firma, Sept. 14–Oct. 11, 1934, *Krukoff 6335* (NY, TYPE, MBG, photograph and analytical drawings).

Perhaps most closely related to *M. hirsuta* (A. Rich.) K. Sch., because of its conspicuously petalaceous bracts, but differing in its narrow corolla-throat and relatively scant indument generally. In shape of foliage and general structure of the corolla *M. Krukovii* displays an affinity with *M. lasiocarpa* (A. DC.) Malme, which, however, has much smaller, lanceolate bracts. Were it not for the fact that *M. hirsuta* has been found to be surprisingly constant throughout a suite of hundreds of specimens representing a majority of extant herbarium specimens, the three species might be suspected as phases of a single, complex entity.

#### V. FORSTERONIA G. F. W. Meyer

- p. 224. To synonymy of *F. leptocarpa* (Hook. & Arn.) A. DC., add:

*Forsteronia rotundiuscula* Miers, Apoc. So. Am. 248. 1878.

- p. 235. To synonymy of *F. thyrsoides* (Vell.) Muell.-Arg. var. *glabriuscula* (A. DC.) Woodson, add:

*Forsteronia divaricata* Miers, Apoc. So. Am. 247. 1878.

- p. 252. To synonymy of *F. corymbosa* (Jacq.) G. F. W. Meyer, add:

*Thyrsanthus pyriformis* Miers, Apoc. So. Am. 100. 1878.

- p. 257. To the list of excluded or doubtful species of *Forsteronia*, add:

*Forsteronia ovalifolia* (Poir.) Miers, Apoc. So. Am. 248. 1878 (*Echites ovalifolia* Poir. Encycl. Suppl. 2: 535.



1811). Perhaps equivalent to *F. spicata* (Jacq.) G. F. W. Meyer, although the latter is apparently unknown from Hispaniola.

*Forsteronia* ? *linearis* (Vell.) Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 107. 1860 (*Echites linearis* Vell. Fl. Flum. 111. 1830; Icon. 3: pl. 36. 1827). Probably a *Forsteronia* but incapable of exact determination.

### IX. ODONTADENIA Benth.

- p. 313. To synonymy of *O. verrucosa* (R. & S.) K. Sch., add:  
*Anisolobus rubidulus* Miers, Apoc. So. Am. 173. 1878.
- p. 317. To synonymy of *O. lutea* (Vell.) Mgf., add:  
*Echites densevenulosa* Stadelm. Flora 24<sup>1</sup>: Beibl. 47. 1841.  
*Anisolobus Salzmanni* A. DC. in DC. Prodr. 8: 395. 1844; Muell.-Arg. in Mart. Fl. Bras. 6<sup>1</sup>: 113. 1860; Miers, Apoc. So. Am. 169. 1878.  
*Anisolobus Stadelmeyeri* Muell.-Arg. loc. cit. 113. 1860; Miers loc. cit. 170. 1878.
- p. 320. To synonymy of *O. puncticulosa* (A. Rich.) Pulle, add:  
*Anisolobus distinctus* Miers, Apoc. So. Am. 169. 1878.  
*Anisolobus oblongus* Miers, loc. cit. 1878.

To the recognized species of *Odontadenia* add the following:

#### ***Odontadenia caudigera* Woodson, spec. nov.**

Fruticosa volubilis; ramulis sat crassiusculis glabriusculis vel minutissime scabridiusculis haud conspicue lenticellatis; foliis oppositis longiuscule petiolatis late ellipticis apice acute breviterque caudato-acuminatis basi late obtusis 14–23 cm. longis 7–11 cm. latis membranaceis opacis glaberrimis; petiolis 2.0–2.5 cm. longis; inflorescentiis lateralibus obscure compositis longe (10–12 cm.) pedunculatis glaberrimis flores 3–6 gilvos speciosos gerentibus; bracteis ovatis 0.2–0.3 cm. longis scariaceis haud caducis; pedicellis ca. 2 cm. longis; calycis laciniis

late ovatis obtusis 0.6–0.7 cm. longis glaberrimis squamellis alternatis 2–3; corollae subinfundibuliformis extus omnino glabrae tubo proprio urceolato 0.8–0.9 cm. longo basi ca. 0.5 cm. diametro metiente faucibus cylindricis 1.6–1.7 cm. longis ostio ca. 0.6 cm. diametro metiente lobis obovato-dolabriformibus rotundatis 2.0–2.1 cm. longis patulis; antheris anguste sagittatis acuminatis 1.2–1.3 cm. longis dorso dense hirtellis; ovario ovoideo ca. 0.2 cm. longo glabro; stigmatibus acute 2-lobatis 0.5 cm. longo; nectariis carnis profunde multidentatis ovarium paulo superantibus; folliculis ignotis.

Stems relatively stout, glabrous or very minutely scabridulous, not conspicuously lenticellate; leaves opposite, petiolate, broadly elliptic, apex acutely and shortly caudate-acuminate, base broadly obtuse, 14–23 cm. long, 7–11 cm. broad, membranaceous, opaque, glabrous; petioles 2.0–2.5 cm. long; inflorescence lateral, obscurely compound, glabrous, bearing 3–6 showy cream-colored flowers; peduncle 10–12 cm. long; bracts ovate, 0.2–0.3 cm. long, scarious, persistent; calyx-lobes broadly ovate, broadly obtuse, 0.6–0.7 cm. long, glabrous, the squamellae in alternate groups of 2–3; corolla subinfundibuliform, glabrous without, the proper-tube urceolate, 0.8–0.9 cm. long, about 0.5 cm. in diameter at the base, abruptly constricted at the insertion of the stamens, the throat cylindrical, 1.6–1.7 cm. long, about 0.6 cm. in diameter at the orifice, the lobes broadly obovate-dolabriform, rounded, 2.0–2.1 cm. long, patulous; anthers narrowly sagittate, acuminate, 1.2–1.3 cm. long, densely hirtellous dorsally; ovary ovoid, about 0.2 cm. long, glabrous; stigma acutely 2-lobed, 0.5 cm. long; nectaries fleshy, deeply multifid, slightly surpassing the ovary; follicles unknown.

BRITISH HONDURAS: data lacking, *Schipp s.n.* (MBG, TYPE).

It is exasperating that no data accompanied the material of this species, supposedly from the interior of the colony. It is readily distinguished from both *O. Hoffmannseggiana* (Steud.) Woods., known only from Costa Rica and Panama in Central America and northern South America, and the Amazonian

*O. stemmadeniaefolia* Woods. by the narrow corolla-throat which gives it the superficial aspect of a member of § *Nitidae*.

## XXVI. PRESTONIA R. Br.

The following species, although included in the Key to Species, has been received too late to be incorporated within the revision proper of the genus:

### ***Prestonia discolor* Woodson, spec. nov.**

Fruticosa volubilis; ramulis crassiusculis glabris; foliis late ellipticis vel late oblongo-ellipticis apice brevissime acuminatis acutisve basi late obtusis 11–21 cm. longis 6–11 cm. latis membranaceis post exsiccationem livide discoloratis opacis omnino glabris; petiolis 1.5–1.8 cm. longis; appendicibus interpetiolaribus sat numerosis late dentiformibus; inflorescentiis corymbosis dichotome divisis flores 30–40 luteo-roseos gerentibus; pedunculo foliis subaequante; pedicellis ca. 1.5 cm. longis glabris; bracteis linearibus ca. 0.08 cm. longis; calycis laciniis elliptico-oblongis acuminatis 1.2–1.3 cm. longis delicate foliaceis glabris squamellis dentiformibus minute erosis vel subintegris; corollae salverformis extus omnino glaberrimae tubo 1.2–1.3 cm. longis basi ca. 0.3 cm. diametro metiente appendicibus epistaminalibus omnino inclusis ca. 0.1 cm. longis faucibus conspicue incrassatis lobis oblique obovatis haud acuminatis 1.4–1.5 cm. longis patentibus; antheris elliptico-sagittatis 0.6 cm. longis dorso distincte pilosulis manifeste exsertis; ovario oblongoideo ca. 0.15 cm. longo glabro; stigmatibus ca. 0.15 cm. longo; nectariis compresse ovoideis basi irregulariter concrecentibus ovarium aequantibus; folliculis ignotis.

Stems relatively stout, glabrous; leaves broadly elliptic to broadly oblong-elliptic, apex very shortly acuminate to acute, base broadly obtuse, 11–21 cm. long, 6–11 cm. broad, membranaceous, lividly discolored in desiccation, opaque, glabrous; petioles 1.5–1.8 cm. long; interpetiolar appendages rather numerous, broadly dentiform; inflorescence corymbose, dichotomously divided, bearing 30–40 yellowish-pink flowers; peduncle about equalling the subtending leaves; pedicels about

1.5 cm. long, glabrous; bracts linear, about 0.08 cm. long; calyx-lobes elliptic-oblong, acuminate, 1.2–1.3 cm. long, delicately foliaceous, glabrous, the squamellae dentiform, minutely erose to subentire; corolla salverform, glabrous without, the tube 1.2–1.3 cm. long, about 0.3 cm. in diameter at the base, the epistaminal appendages wholly included, about 0.1 cm. long, the orifice conspicuously callose-incrassate, the lobes obliquely obovate, not acuminate, 1.4–1.5 cm. long, reflexed; anthers elliptic-sagittate, 0.6 cm. long, distinctly pilosulose dorsally, the tips manifestly exserted; ovary oblongoid, about 0.15 cm. long, glabrous; stigma about 0.15 cm. long; nectaries compressed-ovoid, irregularly conerescent at the base, equalling the ovary; follicles unknown.

BRITISH GUIANA: Mora forest on edge of Karau Creek, Mazaruni River, May 25, 1933, *Tutin 141* (BM, TYPE, MBG, photograph).

Closely related to *P. purpurissata*, but evidently differing specifically in the smaller, greenish calyx-lobes, and shorter corolla-tube with proportionally longer lobes. Mr. Tutin reports that the corolla is yellow and pink, the calyx-lobes green, and the pedicels pale lilac in color.

To the American genera of Echitoideae add the following:

## XXIX. TINTINNABULARIA Woodson

**Tintinnabularia** Woodson, gen. nov. Apocynacearum (Echitoideae).

Calyx majusculus profunde 5-partitus; laciniae foliaceae subaequales margine imbricatae intus basi in marginibus pauciglanduligeræ. Corolla speciosissima magna infundibuliformis; tubus inferne latiuscule cylindricus dein late dilatatus ibique staminiger; limbi laciniae 5 aequales oblique obovatae aestivatione dextrorsum convolutae. Stamina 5 omnino inclusa; antherae inter se adglutinatae et stigmati adplicatae oblongo-sagittatae apice longe caudatae ibique plus minusve convolutae basi obtuse 2-auriculatae dimidia parte superiore ventro pollinigeræ, sporangia uniforme fertilia pollinibus

granulosis; filamenta filiformia antheris conspicue longiora haud adglutinata. Ovarii carpella gemina basi distincta apice in stylo gracili producta ovulis multis in quoque loculo pluri-seriatim positis; stigma capitato-fusiforme apice obscure obtuseque 2-partitum basi 5-maniculatum. Nectarii glandulae 5 saepissime separatae vel inter se plus minusve adglutinatae. Fructus ignotus ut creditur folliculus apocarpus. Frutices volubiles; folia opposita petiolata membranacea supra nervo medio inconspicue glanduligero subtus in axillis nervi medii inconspicue foveata. Inflorescentia lateralis alternata corymbose-trichasialis pluriflora bracteis foliaceis oppositis.

Lactescent (?), fruticose lianas. Stems volubile, terete; branches alternate above. Leaves opposite, membranaceous, the ventral surface bearing rather few, inconspicuous glandular emergences indefinitely clustered at the base of the midrib, the dorsal surface bearing rather inconstantly inconspicuous elliptic foveae in the axils of the midrib; petioles somewhat girdling at the node into a slightly dilated, minutely appendiculate, stipular ring. Inflorescence lateral, alternate, corymbose-trichasial, pluriflorous, the pedicels subtended by solitary, foliaceous bracts. Calyx 5-parted, the lobes subequal, foliaceous, cleft nearly to the receptacle, imbricated, bearing within small groups of alternate, glandular squamellae. Corolla infundibuliform, the tube straight, rather broadly cylindrical below, dilated into a broad throat at the insertion of the stamens, the limb 5-parted, actinomorphic, dextrorsely convolute. Stamens 5, inserted at the base of the corolla-throat, included; anthers connivent and agglutinated to the stigma, consisting of 2 parallel, uniformly fertile sporangia borne ventrally near the apex of an enlarged, caudate, obtusely 2-auriculate connective; pollen granular; filaments very conspicuously longer than the anthers, filiform. Carpels 2, united at the apex by an elongate stylar shaft surmounted by the fusiform-capitate, obtusely 2-lobed, basally 5-maniculate stigma; ovules many, several-seriate, borne upon an axile, binate placenta. Nectaries 5, separate or somewhat irregularly connate. Fruit unknown, supposedly follicular, apocarpous.

***Tintinnabularia Mortonii* Woodson, spec. nov.***Plate 7.*

Fruticosa volubilis altitudine ignota; ramulis teretibus vel leviter compressis glabris maturitate inconspicue lenticellatis; foliis oppositis petiolatis oblongo-ellipticis apice obtuse caudato-acuminatis basi obtusis 9–10 cm. longis 3.0–3.5 cm. latis firme membranaceis omnino glabris supra nervo medio basi inconspicue glanduligeris subtus in axillis nervi medii inconspicue irregulariterque foveolatis; petiolis 0.7–1.0 cm. longis glabris; inflorescentiis corymboso-trichasialibus alterno-lateralibus folia ca. bis superantibus flores speciosos albos ca. 9 gerentibus; pedunculo 4.0–5.5 cm. longo glabro; bracteis foliaceis ovato-lanceolatis acuminatis 1–2 cm. longis; pedicellis 2 cm. longis glabris; calycis laciniis oblongo-ellipticis acuminatis foliaceis 1.2–1.3 cm. longis glabriusculis intus basi squamellas 2–4 minutas alternatas gerentibus; corollae infundibuliformis tubo proprio latiuscule cylindrico 0.7–0.9 cm. longo basi ca. 0.3 cm. diametro metiente extus puberulo-papillato intus prope insertionem staminum dense villosulo faucibus tubularibus 3.0–3.5 cm. longis ostio ca. 0.8 cm. diametro metiente extus intusque dense puberulo-papillatis lobis oblique obovatis obtusiusculis 0.9–1.0 cm. longis extus puberulo-papillatis intus minute denseque puberulis paululo patulis; staminum antheris oblongo-sagittatis caudiculatis basi obtuse 2-auriculatis 1.3 cm. longis caudiculis minute pilosis inter se convolutis filamentis filiformibus 3.5 cm. longis basi minute pilosis; ovariis oblongoideis ca. 0.35 cm. longis glabris; stigmatibus subcapitato basi 5-maniculato ca. 0.3 cm. longo; nectariis compressis ovoideis ovario subaequantibus; folliculis ignotis.

Frutescent lianas of unknown height; branches terete or slightly compressed, glabrous, inconspicuously lenticellate at maturity; leaves opposite, petiolate, oblong-elliptic, apex obtusely caudate-acuminate, base obtuse, 9–10 cm. long, 3.0–3.5 cm. broad, firmly membranaceous, glabrous throughout, upper surface bearing relatively few, inconspicuous glands at the base of the midrib, lower surface bearing with relative in-

constancy solitary elliptic foveae in the axils of the midrib; petioles 0.7–1.0 cm. long, glabrous; inflorescence alternate-lateral, corymbose-trichasial, about twice surpassing the length of the subtending leaves, bearing about 9 showy, cream-colored flowers; peduncles 4.0–5.5 cm. long, glabrous; pedicels 2 cm. long, glabrous; bracts foliaceous, ovate-lanceolate, acuminate, 1–2 cm. long; calyx-lobes oblong-elliptic, acuminate, 1.2–1.3 cm. long, foliaceous, essentially glabrous, the squamellae in alternate groups of 2–4; corolla infundibuliform, the proper-tube rather broadly cylindrical, 0.7–0.9 cm. long, about 0.3 cm. in diameter at the base, puberulent-papillate without, densely villosulose toward the insertion of the stamens within, the throat tubular, 3.0–3.5 cm. long, about 0.8 cm. in diameter at the orifice, densely puberulent-papillate within and without, the lobes obliquely obovate, obtusish, 0.9–1.0 cm. long, somewhat patulous, puberulent-papillate without, minutely and densely puberulent within; anthers oblong-sagittate, caudate, obtusely 2-auriculate at the base, 1.3 cm. long, the convolute apical appendages minutely pilosulose, otherwise glabrous, the filaments filiform, 3.5 cm long, minutely pilosulose toward the base; ovaries oblongoid, rather gradually produced into the style, about 0.35 cm. long, glabrous; stigma subcapitate, basally 5-maniculate, about 0.3 cm. long; nectaries compressed-ovoid, somewhat shorter than the ovary; follicles unknown.

GUATEMALA: ALTA VERAPAZ: quebradas secas, at 2000 ft. alt., in jungle, June 8, 1920, *Johnson 200* (US, TYPE, MBG, photograph and analytical drawings).

The Key to Genera (p. 20†) may be amplified to include *Tintinnabularia* as follows (under A.):

B. Inflorescence bostrychoid, di- or trichotomously compound.

C. Corolla infundibuliform.

D. Calyx-lobes conspicuously foliaceous; staminal filaments filiform, conspicuously longer than the anthers; leaves foveate in the axils of the midrib beneath.....XXIX. TINTINNABULARIA

DD. Calyx-lobes scarious or only slightly foliaceous; staminal filaments shortly cylindrical, shorter than the anthers; leaves not foveate beneath.....I. ALLOMARKGRAFIA

*Tintinnabularia* is of great interest because of its obvious affinity with the Asiatic genus *Beaumontia*, a widely cultivated

liana bearing large, infundibuliform corollas with conspicuously foliaceous calyx-lobes, filiform staminal filaments much longer than the anthers, an anomaly in the Apocynaceae, and leaves which are foveate in the axils of the midrib. *Tintinnabularia* differs from *Beaumontia*, however, in the somewhat smaller corollas with tubular throat and shorter lobes, anthers with convolute apical appendages, carpels which are not united save when immersed within the receptacle, manicate stigmata, and leaves which are glandular at the base of the midrib. Although the fruit of *Tintinnabularia* is not yet known, it is doubtful that it agrees with that of *Beaumontia* which is essentially syncarpous until the dehiscence of the valves.

The specific adjective commemorates Mr. C. V. Morton, who called to my attention the type specimen which had been laid amongst the undetermined exsiccatae of the United States National Herbarium.

## INDEX TO EXSICCATAE

*Italicized* numerals refer to collectors' numbers, *s.n.* (*sine numero*) to unnumbered collections; parenthetical numerals refer to the numerals of taxonomic entities conserved in this revision—the Roman to genera, and the Arabic to species. Varieties are undesignated. Genera Nos. I–IV are contained in Ann. Mo. Bot. Gard. 20: 605–790. (1)–(186). 1933; Nos. V–IX, in 22: 153–306. (187)–(340). 1935; Nos. X–XXIX, in 23: 169–391. (341)–(563). 1936.

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- Duss, P. 2341, 3713 (XXVI 7).
- Dutra, —. 301 (XIII 1).
- Earle, F. S. & C. F. Baker. 2451 (II 9).
- Eastwood, A. s.n. (XIX 1).
- Edwall, L. E. 11147 (V 35); 11242 (VI 1).
- Eggers, H. s.n. (III 81); 438 (V 45); 836 (XVII 1); 1155 (III 96); 1638 (II 7); 1639 (II 8); 1686 (XV 2); 1731 (II 7); 1894, 1894b, 1894c (V 46); 3389 (II 7); 4315 (XV 2); 4707 (XXIII 1); 5297 (XV 1); 5347 (V 41); 5432 (III 81); 5546 (III 96); 5568 (XXVI 14); 13166 (III 81); 14527 (XXVI 40); 14722 (XXVI 60); 14782, 14956 (XXVI 18); 15078 (XXVI 27); 15430, 15430bis (XXVI 16); 15618 (V 26); 15684 (XXVIII 1).
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- Lorentz, P. G. 205 (III 41); 1207 (IV 8).
- Lorentz, P. G. & G. Hieronymus. *s.n.* (III 41); 216, 358 (V 23); 403 (III 41).
- Loz, —. 543 (III 106).
- Luetzelburg, P. *s.n.* (III 43; XXVI 47); 383 (III 30); 5000 (III 74); 6953 (III 70); 7155 (III 44); 12599 (III 30).
- Lund, P. W. *s.n.* (III 25, 74, 76; IV 6, 8, 9; XXVI 17); 886 (IV 10).
- Lundell, C. L. *s.n.* (III 81); 515 (XX 6); 842, 1524 (XVI 2); 1350 (XX 4); 2640 (V 32); 3445, 3533, 4046, 4056, 4736 (XVI 2).
- Luschath, B. *s.n.* (V 3, 34).
- Macbride, J. F. 2777 (II 1); 2785 (XXVI 14); 3730 (III 38); 3902 (XXVIII 1); 4720 (III 81); 5245 (XXVI 8); 5473 (XXVIII 1); 5812 (III 93).
- Mac Nab, G. *s.n.* (VI 6).
- Malmé, G. A. *s.n.* (II 5; III 84; IX 9; XXVI 12); 248, 364 (V 30); 502 (XXVI 2); 602 (V 30); 690 (XIII 1); 827 (XXVI 2); 1038 (V 23); 1058 (II 3); 1118 (VI 1); 1196 (III 84, 96); 1276B (XXVI 47); 1478 (XXVI 8); 1536 (IX 9); 1642 (IX 22); 1766 (IX 21); 2036 (IX 11); 2489 (V 23); 3122 (XXVI 8); 3305 (IX 22).
- Mandon, G. 1472 (III 40).
- Manso, A. da S. *s.n.* (VI 1); 2 (III 86); 398 (III 74).
- Manso, A. da S. & J. Lhotzky. 39 (III 96); 33 (XXVI 12); 34 (II 5); 37 (XXVI 8).
- Martin, J. *s.n.* (III 78; V 12; VIII 10; IX 19; XXIII 3).
- Martius, P. von. *s.n.* (III 30, 72, 74; V 8, 22, 23; VI 4; IX 1, 12, 22; XXIV 1; XXVI 8); 105 (VIII 6); 182 (V 22); 292 (III 74); 293, 299 (III 72); 300 (III 46); 307 (III 71); 324 (VIII 7); 503 (III 74); 504 (III 76); 506 (III 69); 909 (III 46); 966 (VIII 7); 967 (VI 1); 1034 (IX 17); 2267 (III 30); 2663 (IX 5); 2960 (V 7); 3029 (XXVI 29).
- Matthews, A. *s.n.* (XXVI 18); 820 (III 23); 1327, 1977 (III 81); 1978 (III 22).
- Maxon, W. R. & A. D. Harvey. 6507 (II 1); 6527 (III 96).
- Maxon, W. R., A. D. Harvey & A. T. Valentine. 7614 (XX 3).
- Maxon, W. R. & E. P. Killip. 394 (XV 1); 1440 (XVI 1); 1615 (XX 6); 1675 (III 9).
- Maxon, W. R. & A. T. Valentine. 6972 (III 96).
- Mayerhoff, C. J. 28 (II 7).
- Mc Clatchie, A. J. *s.n.* (XIX 1).
- Mc Rae —. *s.n.* (VIII 7).
- Mearns, E. A. 1755 (IV 2); 1884 (IV 2).
- Melinon, —. *s.n.* (VIII 10); 460 (V 12).
- Mellichamp, J. H. *s.n.* (VII 1).
- Mendonça, R. 506 (IV 9).
- Mexia, Y. 5234 (V 47); 5234A (VI 4); 5337 (XXVI 4); 5914 (V 47); 5994 (VIII 5).
- Miers, J. 98 (III 96); 2418 (III 30); 3436 (III 43); 4020 (XXI 2); 4022 (III 96); 4027 (VIII 7); 4029 (III 43); 4031 (III 96); 4049 (V 8).
- Mikan, J. C. *s.n.* (III 49; VIII 7; XIII 4; XXVI 2).
- Millsapough, C. F. 1102, 1113 (II 9).

- Mohr, C. *s.n.* (VII 1).  
 Mohr, C. & —. Sudworth. *s.n.* (VII 1).  
 Moldenke, H. N. 725 (XVII 1); 399A (XV 2); 1006A, 5781 (XVI 1).  
 Montes, M. N. & A. E. Salazar. 486 (IV 3).  
 Moore, J. A. & J. A. Steyermark. 3243 (IV 5).  
 Moore, S. 819 (XXVI 30).  
 Moritz, J. W. K. 31 (III 98); 1153 (III 81); 1899 (III 91).  
 Morong, T. 380 (II 3); 420 (IV 10); 490A (IV 8); 810 (V 23); 895 (II 3).  
 Morton, C. V. & —. Makrinus. 2348 (XXVI 44).  
 Mosén, H. 632 (XIII 4); 947 (III 68); 1461 (XXVI 48); 3020 (XXI 2); 3193 (III 43); 3433 (XXVI 3); 3434 (V 27); 4269 (XXVI 2); 4271 (V 34).  
 Moss, A. M. *s.n.* (III 96).  
 Munies, F. 94 (IV 7); 3586 (V 30).  
 Munz, P. A. 6094 (XIX 1).  
 Mutis, J. C. *s.n.* (III 26, 28); 97 (III 85).  
 Nash, G. V. 135 (XVI 1); 136 (II 8); 138 (XX 6); 158, 286, 584 (II 7); 789 (II 8); 940, 996 (II 7).  
 Nash, G. V. & N. Taylor. 898 (XVI 1); 1309, 1385 (II 7); 1633, 3773 (XVI 1); 3890 (XX 6).  
 Nelson, E. W. 809, 866 (III 81); 3080 (XX 1); 3337 (III 2); 4658 (III 11); 4659 (IV 3); 4692 (IV 5).  
 Netto, L. do S. M. *s.n.* (III 69); 46 (VI 1).  
 Nichols, G. E. 162 (III 9).  
 Niederlein, G. 67b, 72, 83 (V 30); 92 (IV 7); 1965 (V 47); 2319 (V 34).  
 Norman, C. 199 (III 9).  
 Novacs, J. C. 384 (V 35); 11203 (XXVI 4); 11207 (XXVI 59).  
 Nurse, H. A. 3158 (III 81).  
 Oechioni, —. 4459 (VIII 7).  
 d'Orbigny, A. C. V. 879 (IX 12).  
 Ørsted, A. S. 15510 (III 37); 15542 (II 1); 15544 (XX 1).  
 Ortega, J. G. 4719 (IV 3).  
 Ortenburger, A. I. *s.n.* (VII 1).  
 Osta, —. 1014 (III 48).  
 Ostenfeld, C. 334 (II 7).  
 Owen, —. 1 (XXVI 43).  
 Pabst, C. 557 (V 27).  
 Palmer, E. 28 (IV 3); 98 (III 7); 205 (IV 2); 238 (III 11); 259 (XXII 1); 296 (IV 3); 395 (III 11); 447 (IV 3); 571, 605, 697 (III 10); 702 (IV 4); 724 (III 11); 734 (III 13); 805 (III 10); 807 (IV 4); 841 (IV 1); 1028 (XXVI 55); 1127 (III 10).  
 Palmer, E. J. 438 (XX 6); 6063, 7958, 8089 (VII 1); 10018, 10243 (IV 5); 10537 (VII 1); 10995 (IV 5); 16460, 16542, 23132, 27116, 29164, 39314 (VII 1).  
 Palmer, W. & J. H. Riley. 207, 337 (XV 2); 348 (II 9); 364, 833 (XVI 1); 842 (XX 6); 871 (II 9); 1010 (XVI 1); 1041 (XX 6).  
 Parker, C. S. *s.n.* (III 96); 259 (III 86).  
 Parry, C. C. & E. Palmer. 574 (IV 3).  
 Passarge, S. 86 (III 100).  
 Passarge, S. & —. Selwyn. 287 (IX 21).  
 Pavon, J. *s.n.* (III 2, 19, 33, 38, 81; XXVI 16, 55; XXVIII 1); 389 (II 4).  
 Pearce, R. *s.n.* (III 23); 708 (III 60).  
 Peck, M. E. 35 (III 81); 450 (V 11); 653 (XXVI 38); 671 (VIII 20); 696 (III 96).  
 Peckholt, T. 18 (IV 9); 559 (XXVI 50).  
 Pennell, F. W. 1330, 1390 (III 81); 1525 (II 1); 1633 (III 81); 2034 (III 27); 2726, 2817 (III 85); 3438 (II 6); 3442 (III 85); 3911 (II 2); 3912 (XXVI 8); 3956 (XVII 3); 4155, 4181, 4617 (II 1); 5405 (III 91); 5604 (III 95); 5719 (XXVI 22); 10231, 10703, 10783, 10820 (III 91); 10884 (II 1, 6); 12002 (II 1).  
 Pennell, F. W., E. P. Killip & T. E. Hazen. 8686 (III 91).

- Perkins, J. R. 276 (III 9); 1100, 1378 (V 43).  
 Perrottet, S. *s.n.* (II 1; III 78; VIII 10); 270 (IX 12); 273 (III 96).  
 Persaud, —. 74 (III 88).  
 Picarda, L. 154 (V 46); 804 (XXIII 2); 813 (V 46).  
 Pickel, D. B. 1222 (V 27).  
 Pilger, R. 643 (IV 6); 670 (III 96); 799 (VI 1).  
 Piper, C. V. 5350 (II 1); 5914 (III 96).  
 Pittier, H. *s.n.* (III 96); 144 (III 3); 203 (III 96); 304 (III 81); 343 (III 96); 369 (III 37); 471 (II 1); 520 (III 93); 555 (III 96); 611 (III 95); 810 (III 81); 2498 (III 96); 2813 (VIII 20); 3147 (III 37); 3736 (III 82); 3753 (VIII 20); 3767 (XXVI 37); 3976 (IX 19); 4002 (III 96); 4329 (IX 1); 4417 (II 1); 4700 (XXVI 49); 4756 (III 86); 4941 (II 1); 5125 (XIII 5); 5460, 5490 (III 96); 6047 (XXVI 14); 6652 (XXVI 57); 6869 (II 1); 7300 (III 81); 7598 (III 82); 7638 (II 1); 8108 (III 61); 8540 (III 96); 8832 (XXVI 52); 8918 (V 4); 8920 (XIII 3); 9650 (III 81); 9730 (II 1); 9881 (IX 19); 9935 (XXVI 44); 10127 (III 98); 10760, 11212 (II 1); 11222, 11278 (III 81); 11551 (Ad-denda); 11597 (III 81); 13037 (II 1); 12401 (XXVI 44); 12556 (III 61); 12558 (III 81); 12759 (II 1); 12778 (III 81); 13121 (II 1); 13412 (XXVI 14); 13436 (III 96); 16016 (XXVI 44); 16137 (VIII 20); 16622 (V 32).  
 Poeppig, E. 33 (II 4); 144 (III 81); 537 (XV 2); 1233 (III 81); 1582 (VI 2); 1840 (III 83); 2161 (XXVI 30); 2547 (VIII 10); 2667 (IX 10); 2946 (XVII 1).  
 Pohl, J. E. *s.n.* (III 21, 30, 58, 72, 74, 76; IV 9; V 27; VI 1; XXVI 47); 15 (III 43); 895 (IV 10); 970 (IV 6); 1383 (IX 9); 1592 (XIV 1); 1845 (VI 1); 1846 (VI 4); 1898 (IX 22); 1899 (IX 9); 3189 (V 23); 2214 (XXVI 47); 2453 (XXVI 2); 5167 (XXVI 50); 5168, 5397 (XXVI 2).  
 Poiteau, A. *s.n.* (II 1, 8; III 96; V 12).  
 Pollard, C. L., E. Palmer, & W. Palmer. 2, 218 (II 9).  
 Pollard, R. M. 10 (III 86).  
 Porto, —. 7931 (IV 9); 8671 (VIII 7).  
 Preuss, P. 1462 (III 96); 1617 (XXVI 47).  
 Pride, —. *s.n.* (III 55).  
 le Prieur, F. R. *s.n.* (III 78, 86, 96); 241 (III 78); 244 (III 96).  
 Pringle, C. G. *s.n.* (III 8); 320 (IV 3); 690 (III 11); 694 (IV 5); 701 (III 11); 1108, 4393 (IV 3); 4662 (III 32); 4822 (XXV 3); 5422 (III 7); 6224 (XXVI 55); 6329 (III 7); 6341 (XXVI 55); 6554 (XXVIII 3); 6966, 7242 (XXV 2); 11014 (IV 3); 11015 (III 11); 11357 (III 13); 11838 (IV 4); 13106 (III 8); 13585 (XXV 4); 13760 (III 32); 13890 (III 8).  
 Pulle, A. A. 73 (III 86); 291, 453 (V 12); 493 (III 78).  
 Purdie, W. *s.n.* (II 1; III 9, 26, 81).  
 Purpus, C. A. 251 (XIX 1); 1378 (IV 4); 1392 (III 10); 1935 (III 1); 2215 (III 81); 3989 (IV 4); 4613 (III 10); 5055, 5206 (IV 4); 5213 (III 10); 5408 (XXII 1); 5906 (III 81); 6233 (XXII 1); 6929 (III 82); 7274 (III 6); 7281 (III 81); 7665 (XXVI 55); 10347 (V 41); 10739 (III 81); 10790 (III 1); 10885 (III 81); 11134 (XXVI 55).  
 Queleh, J. J. & F. N. McConnell. 132 (III 89); 146 (III 94); 194 (III 89).  
 Raben, (Graf) F. C. *s.n.* (III 74).  
 Raimondi, A. 2228 (XXVI 51).  
 Ravenel, H. W. *s.n.* (VII 1).  
 Record, S. J. *s.n.* (III 81).  
 Regel, —. *s.n.* (V 24; VIII 6; XXVI 35).

- Regnell, A. F. *II* 186 (III 25); 189 (III 96; IV 10); 280 (III 72); 287 (III 74); *II* 358 (XXVI 2); *III* 850 (IX 9); *II* 873 (III 30); 874 (III 77); 875 (III 68, 76); *III* 877 (V 35); 878 (IV 9); *III* 880 (IX 9); 881 (II 5); *III* 882 (V 30); *III* 883 (XIII 4); *III* 884 (XXVI 59); *III* 885 (XXVII 1); 1462 (III 86); *III* 1600 (XXVI 48).
- Reiche, C. *s.n.* (III 11).
- Reineck, E. M. 467 (V 30).
- Reineck, E. M. & J. Czermak. 467 (V 27).
- Reko, B. P. 3411 (III 81); 3511 (XXII 1); 3955 (III 32); 4823 (XXV 1); 5166 (III 11); 5212 (IV 4).
- Reverchon, J. 1373 (IV 5); 2553 (VII 1).
- Rovirosa, J. N. 126, 225 (III 81).
- Reynolds, H. S. *s.n.* (VII 1).
- Richard, —. *s.n.* (VIII 11).
- Ricketts, —. *s.n.* (IV 2).
- Ridley, H. N., T. S. Lea & G. Ramage. *s.n.* (III 96).
- Riedel, L. *s.n.* (II 5; III 21, 30, 58, 72, 74, 76, 96; IV 8, 10; V 8, 22, 27, 34; VI 1; VIII 6, 7; XIII 4; XXVI 2; XXVII 1); 60, 61 (III 43).
- Rimbach, A. 22 (II 1).
- Ritter, —. *s.n.* (XVII 1).
- Rodriguez, —. 605 (V 34); 3588 (V 30).
- von Rohr, J. P. B. *s.n.* (III 78); 23 (XXVI 7).
- Roig, J. T. 109 (X 1); 3227 (X 2).
- Rojas, T. 2 (II 3); 2654 (IV 8); 9698 (V 23); 9768A (XXVI 59); 9833 (XIII 2); 10270 (XXVI 8); 10653 (V 47).
- Rose, J. N. 1716 (XXVIII 3); 1933, 3474 (IV 3); 16700 (IV 1).
- Rose, J. N., W. R. Fitch & P. G. Russell. 4292 (XX 6).
- Rose, J. N. & R. Hay. 6292 (IV 3).
- Rose, J. N. & —. Hough. 4753 (IV 3).
- Rose, J. N., —. Pachano & J. S. Rose. 23039 (III 35).
- Rose, J. N., J. H. Painter & J. S. Rose. 9055, 9129 (III 10); 9510 (III 11).
- Rose, J. N. & J. S. Rose. 22592 (III 57).
- Rothrock, J. T. 146, 369 (III 9); 497, 646 (IV 2).
- Rothschub, E. 614 (III 81).
- Rudolph, B. *s.n.* (III 86).
- Rugel, F. *s.n.* (VII 1); 114 (XVII 1); 343 (V 46); 397 (XXIII 1).
- Rusby, H. H. 2379, 2380 (III 79); 2385 (III 23, 90); 2386 (III 40); 2387 (III 96); 2392 (VI 1); 2393 (II 4); 2394 (III 39, 73); 2526 (V 23); 2694 (III 73).
- Rusby, H. H. & F. W. Pennell. 121 (XXVI 15); 404, 1032 (III 85).
- Rusby, H. H. & R. W. Squires. 20 (XVII 3); 293 (III 78); 302 (XXVI 8).
- Ruth, A. 482 (VII 1).
- Saer, —. *s.n.* (III 81).
- Sagot, P. A. 321 (III 96); 322 (III 78); 323 (IX 19); 326 (III 86); 327 (XVII 1); 322 (VIII 10); 326 (III 88); 1067 (V 12); 1143 (VIII 10).
- de la Sagra, R. *s.n.* (XV 2; XVII 1); 120 (II 9).
- St. Hilaire, A. de. 2597 (IV 8).
- Salazar, A. E. *s.n.* (III 11).
- Salzmänn, P. 318 (III 43); 320 (III 86).
- Sampaio, A. J. de. 232 (III 96).
- Samuels, J. A. 439 (V 9); 457 (III 88).
- Sandwith, N. Y. 283 (VIII 10); 334 (V 40); 405 (V 12); 416 (V 38); 467 (V 1); 553 (IX 15).
- Sartorius, K. *s.n.* (III 81).
- Schaffner, W. 489 (IV 3).
- Schenck, H. 1875 (V 27); 1947 (XXVI 35); 2269 (V 27).
- Schiede, C. J. W. 167 (III 81); 448 (III 11); 488 (XXVI 55); 493 (III 11).
- Schipp, W. A. *s.n.* (XXVIII 4; Ad-denda); 56 (III 96); 143 (XVII 1); 360 (V 11); 368 (III 81); 376 (XVII 1); 491 (XVI 2); 953 (VIII 20);

- S-7* (XXVI 56); *S-47* (II 1); *S-388* (XXVI 42).
- Schlim, L. J. *510* (VI 3).
- Schomburgk, Rich. *200* (IX 21); *854* (V 15); *1438* (V 38); *1514* (V 9).
- Schomburgk, Robt. H. *s.n.* (XI 3); *22* (II 7); *37* (V 9); *39* (VIII 10, 16); *130* (III 96); *183* (III 103); *309* (IX 19); *311* (II 1); *329* (XVII 2); *350* (III 87); *374* (XXVI 47); *383* (III 89); *421* (VI 1); *557* (V 9); *599* (VI 1); *608* (V 1); *665*, *681* (VI 1); *707* (V 38); *713* (XXVI 9); *725* (V 15); *755* (XXVI 47); *782* (V 9); *788* (VIII 10); *800* (VIII 10); *821* (V 12); *830* (VIII 3); *951* (VIII 10); *953* (V 1, 18); *1378* (VIII 10); *1386* (VIII 3); *1446* (V 12); *1551* (XI 2); *1953* (III 106).
- Schornbaum, —. *s.n.* (V 27).
- Schott, A. *673* (III 9).
- Schott, H. W. *s.n.* (VIII 7); *5339* (XXVI 19); *5398* (XIII 4); *5404* (III 43); *5976* (V 3).
- Schüch, C. G. de. *s.n.* (XXVI 4).
- Schultze, A. *193* (III 85); *245* (XXVI 15); *474* (XXVI 26); *605* (XXVI 49).
- Schunke, C. *389*, *391* (III 79).
- Schwacke, W. *8754*, *11854* (V 35).
- Seemann, O. *95* (III 82); *156*, *161* (II 1); *1330* (III 37).
- Seitz, A. *14* (III 96).
- Seler, C. & E. Seler. *39* (III 32).
- Sello[w], F. *s.n.* (III 25, 64, 69, 75; IV 7, 8; V 2, 8, 22, 47; VI 1; VIII 6; XXVI 19, 35); *34* (III 62); *35* (XXVI 2); *36* (V 35); *169* (III 43); *170* (III 96); *211* (V 8); *212* (III 86); *217* (III 43, 96); *219* (V 8); *358* (V 8); *388* (V 27); *396* (V 22); *460* (V 28); *543* (V 8); *550* (XXVI 50); *635* (V 34); *693* (IV 8); *791* (III 43); *998* (III 96); *1313* (III 30); *1406* (XXVI 48); *1473* (V 30); *1493* (III 76); *1642* (V 27); *1656* (III 69); *1658* (III 72); *1662* (III 30); *3203* (III 76); *4500* (IV 10); *4502* (III 76); *4801* (III 74).
- Selwyn, —. *80* (III 100).
- Setchell, W. A. & C. C. Dobie. *s.n.* (XIX 1).
- Shafer, J. A. *13* (X 1); *297* (XVI 1); *302* (XX 6); *493*, *941* (II 9); *1236* (XX 6); *1281* (X 1); *1447* (V 46); *1500* (II 9); *1624* (XVI 1); *3446* (II 9); *2590* (XX 6); *2737* (XVI 1); *2748* (XVI 1); *2872* (V 46); *2928* (II 10); *2951* (XX 6); *2955* (II 10); *3106* (X 1); *7970* (XX 6); *8268* (X 1); *10370* (XX 6); *10383* (II 9); *10428* (XV 2); *11861* (II 9); *11966* (X 1); *12167*, *13419* (XX 6).
- Shannon, R. C. & E. S. Shannon. *28* (XVIII 1).
- Shannon, W. C. *218*, *251* (III 82).
- Shattuck, O. *129* (XXVI 37).
- Shaw, —. *s.n.* (III 72).
- Sieber, F. W. *92* (III 81); *333* (III 96); *373* (II 1).
- Simpson, J. H. *251* (XV 2).
- Sintenis, P. *273* (V 45); *273C* (XVI 1); *1622* (V 45); *1891* (XVI 1); *2457* (XXVI 1); *2866*, *5195*, *5306*, *5357*, *6223* (V 45).
- Siquiera, R. *21623* (V 12); *21633* (XXVI 46); *21771* (VIII 5).
- Small, J. K. *3995*, *3786* (XVI 1).
- Small, J. K. & J. J. Carter. *2654* (XVI 1); *2655*, *2657* (XX 6); *3116*, *3605* (XVI 1); *8751* (X 3).
- Small, J. K., J. J. Carter & G. K. Small. *3545* (XX 6).
- Small, J. K., C. A. Mosier & G. K. Small. *6532* (XX 6).
- Small, J. K. & G. V. Nash. *s.n.* (XX 6).
- Small, J. K. & P. Wilson. *1756* (XVI 1).
- Smith, A. L. *672* (III 12).
- Smith, C. L. *71* (III 96).
- Smith, H. H. *165* (XXVI 47); *834* (V 41); *1640* (II 2); *1641*, *1642* (II 1); *1643* (XXVIII 2); *1644* (XXVI 14); *1645* (XXVI 8); *1647* (XXVI 26); *1656* (XXVI 53); *1662* (III 81);

- 1904 (III 36); 2412 (XIII 3); 2413 (III 81); 2525 (XXVIII 2); 6663 (III 95).
- Smith, J. D. 1746 (III 96); 4884, 6657 (III 96).
- Smith, L. B. 1529 (III 67); 2037 (XXI 2).
- Smith, L. C. 257, 468 (III 33); 660 (III 81); 661 (XXVI 55); 691 (III 81).
- Snethlage, E. H. 328 (II 1).
- Sodi, A. s.n. (XXVI 18); 10613, 10616 (III 17); 10617 (XXVI 27); 10716 (XXIV 2).
- Splitgerber, —. s.n. (III 96).
- Spruce, R. s.n. (III 29, 81, 86, 108; IX 9; XVII 1); 229 (III 96); 239 (XXVI 33); 551 (II 1); 680 (IX 22); 999 (V 18); 1002 (XXVI 8); 1003 (VIII 11); 1348 (II 1); 1566 (VIII 11); 1615 (IX 19); 1672 (VIII 19); 1882 (XXVI 34); 2080 (V 18); 2083 (IX 23); 2206 (III 86); 2305 (VIII 11); 2435 (VIII 10); 2472 (VIII 17); 2503, 2555 (IX 5); 2595 (VIII 14); 2748 (IX 4); 2863 (III 108); 3051 (III 82); 3136 (XI 2); 3152 (IX 23); 3305 (VIII 12); 3395 (III 105); 3430 (XXVI 8); 3481 (V 10); 3550 (IX 5); 3610 (III 104); 3718 (XI 1); 4303 (III 101); 4493 (V 5); 4900 (IX 18); 4908 (V 31); 5390 (III 26); 6019, 6484 (XXVI 18); 6485 (II 1).
- Stahel, —. & —. Gonggrijp. 3862 (IX 23); 6624 (V 12).
- Stahl, A. 713 (V 45).
- Standley, P. C. 22349 (XXVI 44); 23512 (XXII 1); 23673 (XXVI 58); 24513 (III 81); 25027 (III 96); 27717, 27936 (II 1); 28636 (VIII 20); 29251 (II 1); 30184 (VIII 20); 30290 (II 1); 30385 (III 96); 30562, 31810 (II 1); 41332 (XXVI 57); 53619 (II 1); 54737 (VIII 20); 56365, 56470 (III 81).
- Steere, W. C. 1471 (XX 4); 1477 (XX 5); 1918 (XVI 2); 1987 (XX 6).
- Steinbach, J. 2863 (XXVI 28); 3113 (VI 1); 3256, 3331 (XXVI 8); 3772, 6065 (XXVI 59); 6717 (V 20); 6813 (XXIV 1); 7272 (XXVI 24); 7295 (V 23); 7301 (VI 1); 7376 (XXVI 28); 7456 (II 5); 7577 (III 96); 7782 (V 23); 8020 (V 20); 8662 (III 40); 9090 (III 23).
- Stephan, —. s.n. (III 76, 96).
- Stevens, E. P. s.n. (III 96).
- Stevens, F. L. 538 (III 81); 1006 (III 82).
- Stewart, J. T. s.n. (VII 1).
- Stork, —. 270 (III 96).
- Stuckert, T. s.n. (IV 8).
- Stuebel, A. 56 (III 53); 74 (III 85).
- Sutcliffe, E. C. s.n. (XIX 1).
- Swartz, O. s.n. (III 9; V 43; XV 1; XXVI 1).
- Tafalla, —. s.n. (I 1).
- Talbot, H. F. s.n. (III 78).
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N. B. As the final section of "The American Genera of Echitoideae" goes to press the type specimens of Sessé & Mocifio's ambiguous species of *Echites* are received from Madrid through the courtesy of Mr. Paul C. Standley, of the Field Museum of Natural History, Chicago. As a result these poorly understood entities may now be assigned definite status in many instances, although too late to be included within the present account. A subsequent paper concerning them will be published in the near future.

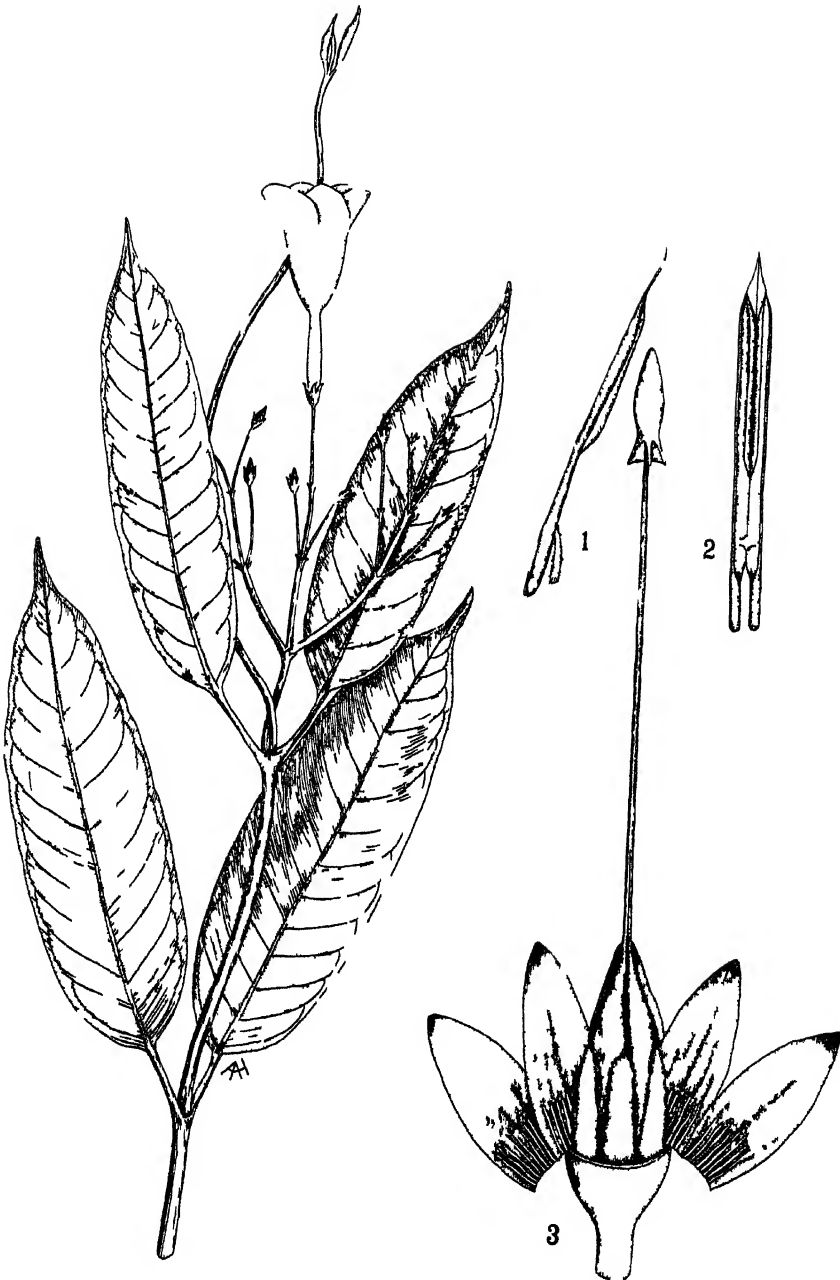


## EXPLANATION OF PLATE

## PLATE 1

*Allomarkgrafia ovalis* (Mgf.) WoodsHabit ( $\times \frac{3}{4}$ ) and dissection of calyx and reproductive organs ( $\times 10$ )

- Fig 1. Anther, side view.  
Fig 2. Anther, ventral view  
Fig 3. Dissected calyx, showing internal squamellae, nectaries, ovary, style, and stigma.



## EXPLANATION OF PLATE

## PLATE 2

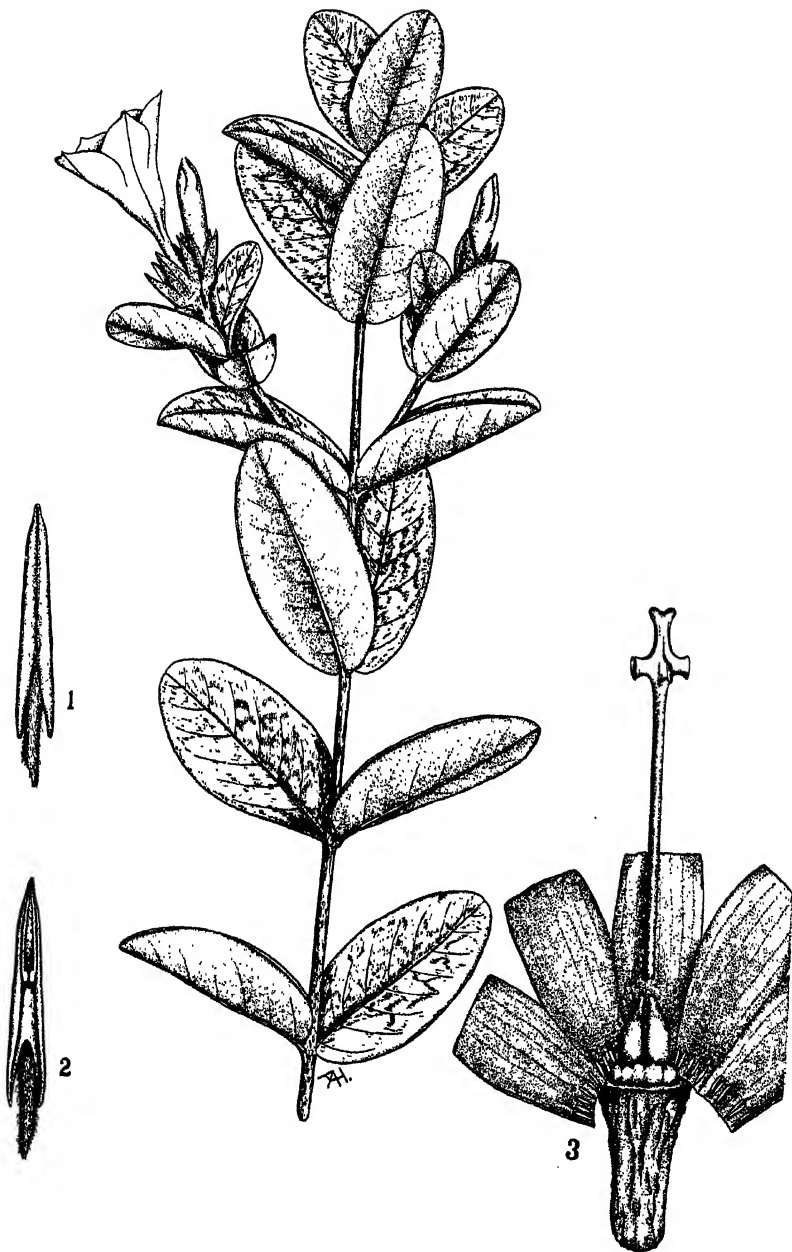
*Galactophora calycina* (Hub.) Woods.

Habit ( $\times \frac{3}{8}$ ) and dissection of calyx and reproductive organs ( $\times 5$ ).

Fig. 1. Anther, dorsal view.

Fig. 2. Anther, ventral view.

Fig. 3. Dissected calyx, showing internal squamellae; nectaries, ovary, style, and stigma.



## EXPLANATION OF PLATE

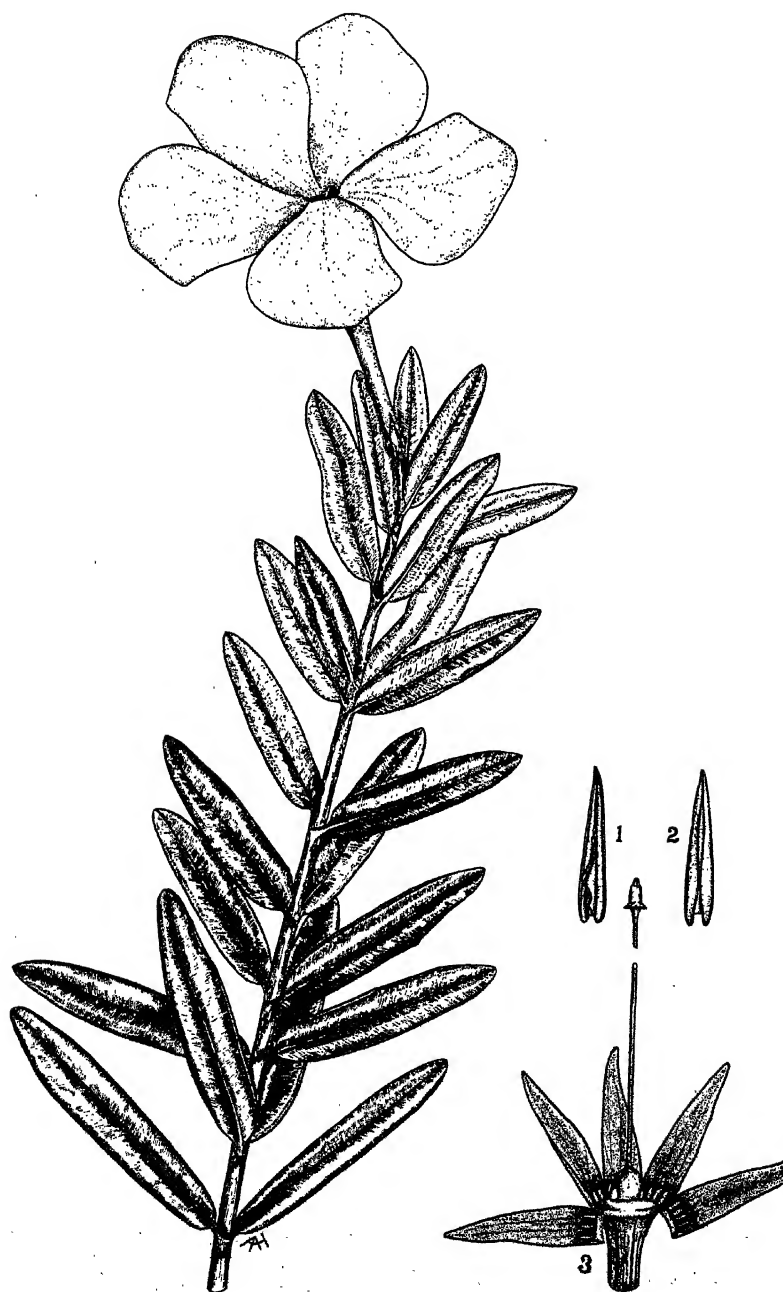
## PLATE 3

*Salpinctes kalmiaefolius* Woods.Habit ( $\times 1$ ) and dissection of calyx and reproductive organs ( $\times 5$ ).

Fig. 1. Anther, ventral view.

Fig. 2. Anther, dorsal view.

Fig. 3. Dissected calyx, showing squamellae; nectaries, ovary, style, and stigma.



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## EXPLANATION OF PLATE

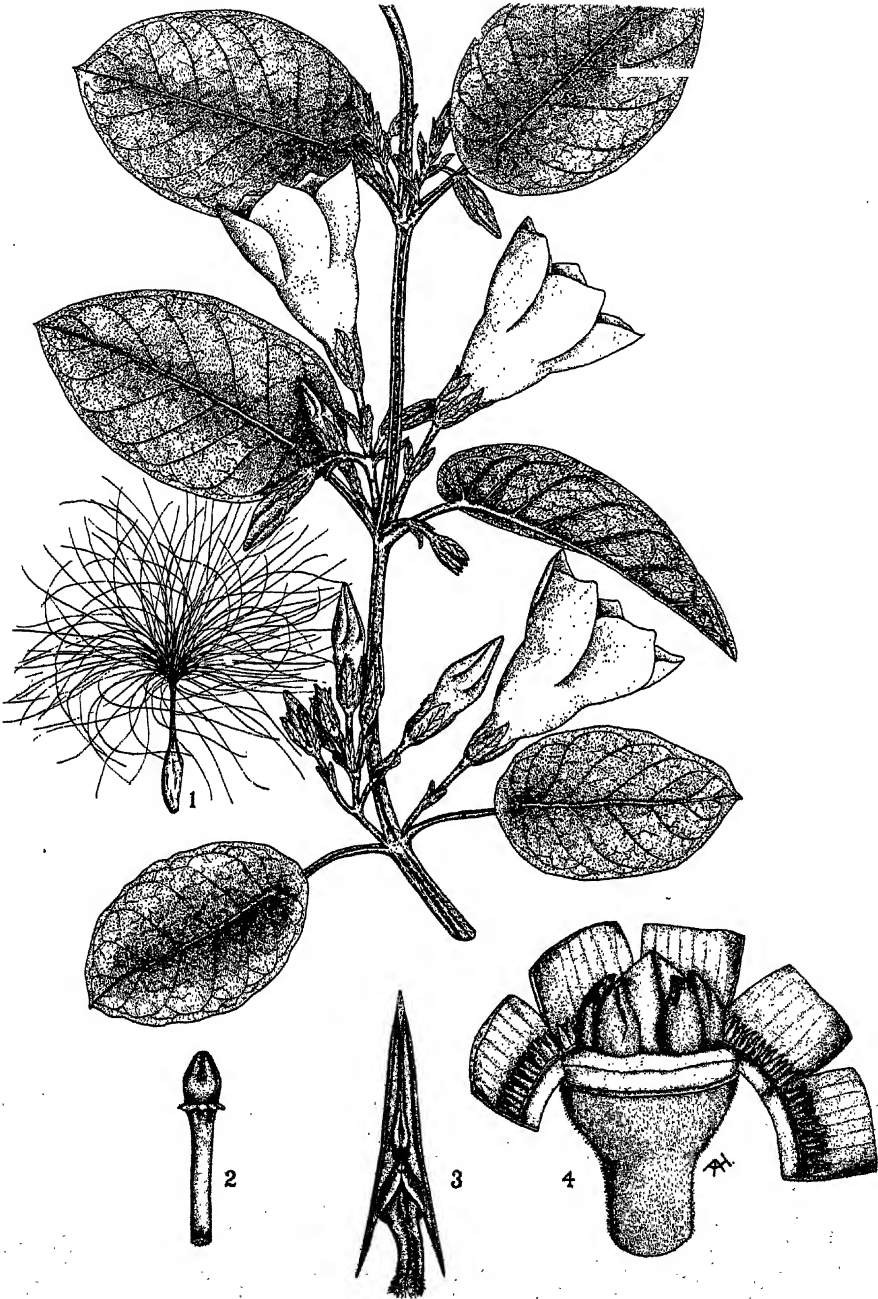
## PLATE 4

*Peltastes malvaeflorus* Woods.Habit ( $\times \frac{1}{2}$ ) and dissection of calyx and reproductive organs ( $\times 4$ ).Fig. 1. Seed ( $\times 2$ ).

Fig. 2. Stigma and portion of style.

Fig. 3. Anther, ventral view.

Fig. 4. Dissected calyx, showing squamellae; nectaries and ovary.



## EXPLANATION OF PLATE

## PLATE 5

*Fernaldia pandurata* (A. DC.) Woods.Habit ( $\times \frac{2}{3}$ ) and dissection of calyx and reproductive organs ( $\times 5$ ).

Fig. 1. Anther, ventral view.

Fig. 2. Anther, side view.

Fig. 3. Stigma.

Fig. 4. Dissection of calyx, showing squamellae; nectaries and ovary.



## EXPLANATION OF PLATE

## PLATE 6

*Asketanthera calycosa* (A. Rich.) WoodsHabit ( $\times \frac{2}{3}$ ) and dissection of calyx and reproductive organs ( $\times 4$ ).

- Fig. 1. Anther, dorsal view
- Fig. 2. Anther, ventral view.
- Fig. 3. Stigma and portion of style
- Fig. 4. Dissected calyx, showing squamellae; nectaries and ovary

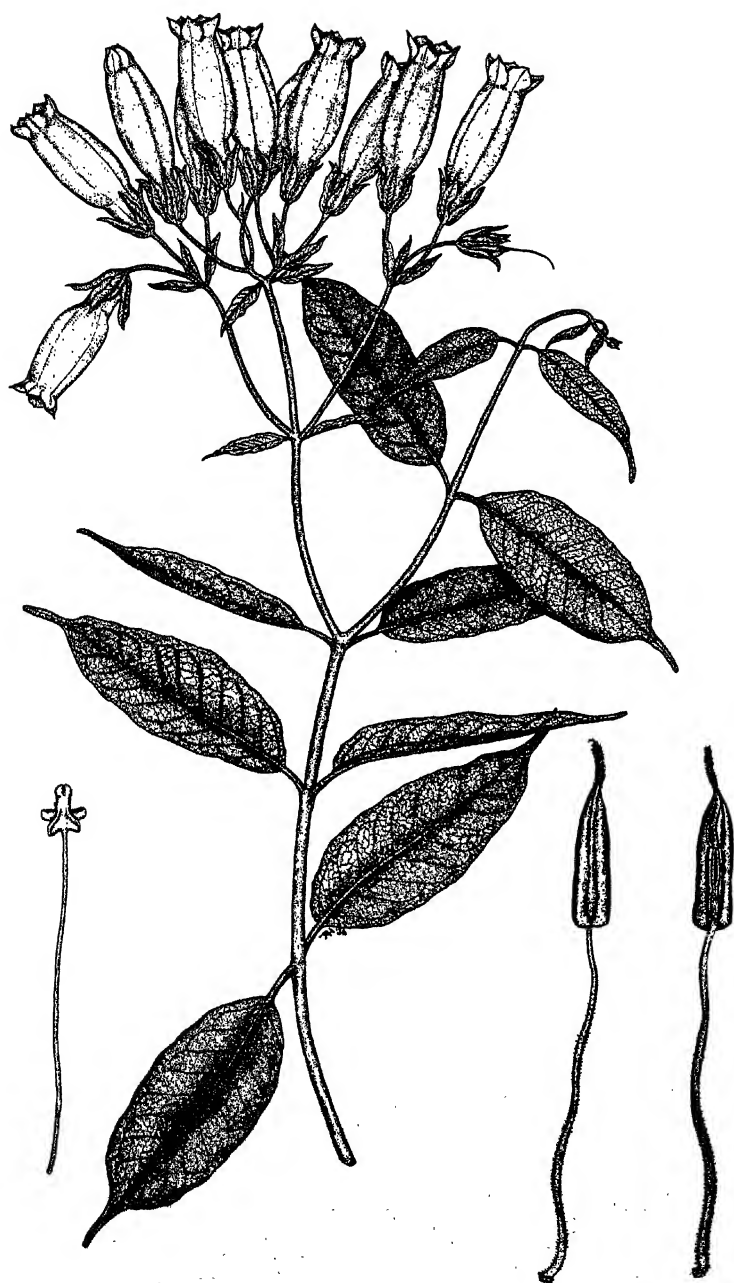


## EXPLANATION OF PLATE

## PLATE 7

*Tintinnabularia Mortonii* Woods.Habit ( $\times \frac{2}{5}$ ) and dissection of reproductive organs ( $\times 2$ ).

- Fig. 1. Stigma and style.  
Fig. 2. Anther, dorsal view.  
Fig. 3. Anther, ventral view.



WOODSON—STUDIES IN APOCYNACEAE





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## A NEW SEQUOIOXYLON FROM FLORISSANT, COLORADO<sup>1</sup>

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The Miocene lake bed at Florissant, Colorado, has long been recognized for its wealth of fossil plants, insects, and vertebrates. The excellence of the leaf impressions found in these sedimentary deposits is second to few localities in the world and certainly the silicified trunks and stumps, at least as regards size, are unsurpassed. The Florissant flora has been generally accepted by competent paleobotanists as being of Miocene age (Berry, '29, p. 234). More recently, Gazin ('35), in describing a marsupial (*Peratherium* sp.) from this formation, suggests a lower Tertiary age. The weight of evidence at present, however, is in support of the Miocene.

Of the score or more of stumps that have been excavated at the Henderson Petrified Forest (located 2½ miles south of Florissant) one in particular is outstanding because of its magnitude. The stump was mentioned by Gordon ('34) in a recent address before the British Association as follows: "The largest fossil tree I know, and I think it is the largest yet discovered, is a stump said to be of the *Sequoia* type. . . . It is 17½ feet in diameter and 10 feet high, quite comparable in girth, therefore, with the Big Trees of today." Henderson ('06) writes of the abundance of fossil stumps at Florissant and figures one, said

<sup>1</sup> Issued September 1, 1936.

to be a *Sequoia*, which unquestionably is the same one mentioned by Gordon and described in this paper (pl. 20, fig. 1). According to Henderson, unsuccessful attempts were made to cut sections of the trunk for exhibition purposes.

Apparently no anatomical studies of this stump have ever been published despite its unusual interest. The wood is infiltrated with silica and only slightly replaced, the preservation being very good with the exception of the pitting in the radial walls of the ray cells. A few ground sections were prepared, but due to the fragility of the wood satisfactory transverse sections could not be obtained by the usual method. Consequently, small fragments were desilicified in a solution of  $\frac{1}{3}$  hydrofluoric acid and  $\frac{2}{3}$  alcohol for 3–4 days, then embedded in celloidin, and cut on a sliding microtome. Very satisfactory transverse sections were obtained using this method, but desilicification rendered the radial sections of less value than the ground ones.

#### SEQUOIOXYLON PEARSALLII, N. SP.

*Annual rings*.—Well-defined, comprised mostly of large, thin-walled cells, the greater portion of which have been crushed (pl. 20, fig. 3); relatively little summer wood, transition varying from abrupt (pl. 21, fig. 7) to gradual (fig. 6).

*Resin canals*.—Neither normal nor traumatic resin canals observed.

*Wood parenchyma*.—Abundant, more so in late spring and summer wood, diffuse, resinous; cells markedly smaller in diameter than surrounding tracheids.

*Wood rays*.—Few to 30 or more cells high, mostly uniseriate, occasionally biseriate; apparently one to two pits per cross field although the preservation of this feature is very poor, horizontal walls sparingly pitted but no pitting observed in cross (tangential) walls; marginal ray cells larger and more nearly resembling true ray tracheids than the ray parenchyma, also entirely lacking the resinous (?) contents of the latter (text-fig. 1).

*Tracheids*.—Pitting uniseriate (mostly scattered) and biseriate (usually opposite); crassulae not observed; tangential

pitting abundant in late summer wood (pl. 20, fig. 5). Strand tracheids occasionally found in summer wood composed of short tracheary elements interspersed with parenchyma cells, both horizontal and *vertical* septations occur, the vertical septations always extending in a radial direction (pl. 20, fig. 4, pl. 21, fig. 9).

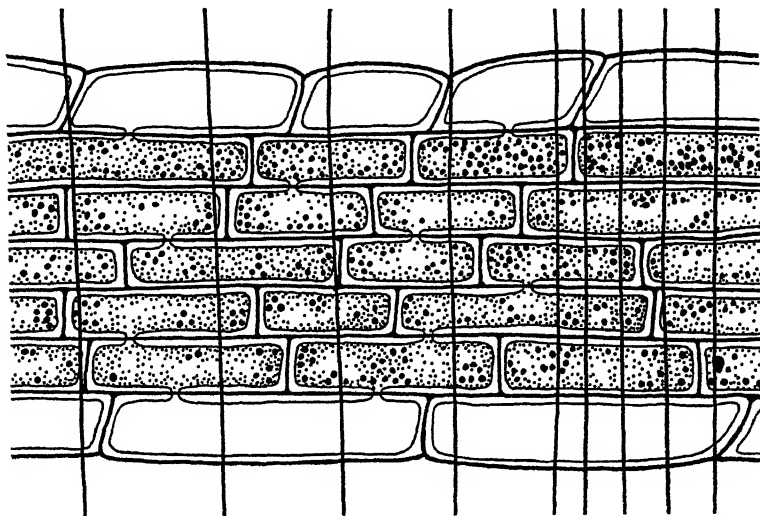


Fig. 1. *Sequoioxylon Pearsallii*. Radial longitudinal view of ray, showing pitting of horizontal walls and differentiated marginal cells.

The species is named for Mr. Cortland Pearsall, of the Massachusetts Institute of Technology, for his valuable assistance in the field and laboratory.

With the exception of the ray structure the general anatomy of the wood indicates a close relationship to *Sequoia*, and although traumatic resin canals have not been observed we feel justified in placing the wood in the genus *Sequoioxylon*. The two most interesting and distinctive features of this wood are the ray structure and the presence of strand tracheids.

The strand tracheids, with their horizontal and *radio-longitudinal* septations composed of short tracheary elements interspersed with parenchyma cells, are, to the writer's knowledge,

a previously undescribed feature in fossil woods. Dr. I. W. Bailey ('34) has described uniseriate strand tracheids in the living redwood (*Sequoia sempervirens*) and has kindly advised the writer that the biseriate type (pl. 20, fig. 4; pl. 21, fig. 9) is of common occurrence in injured crowns of that tree, but apparently figures of the feature have never been published. A band of the strand tracheids is shown in tangential view in the late summer wood in pl. 21, fig. 8 and portions of the same are shown more highly magnified in pl. 20, fig. 4 and pl. 21, fig. 9. The longitudinal septations extend only radially as may be seen by their complete absence in radial section (pl. 20, fig. 2). As this feature is not of constant occurrence at the end of every ring it is doubtful whether it is of any phylogenetic significance; it is more likely that the longitudinal septations are the result of traumatism.

The differentiation of the marginal ray cells is a constant feature and not merely of sporadic occurrence as in the living *Sequoia*. Although not true ray tracheids they are usually distinctly larger than the remainder of the ray cells, more nearly resemble true ray tracheids in shape, and are entirely lacking the ergastic or resinous (?) contents characteristic of most of the ray cells (text-fig. 1).

The wood under consideration seems to resemble *Sequoia Penhallowii* Jeffrey more closely than any other described species of Sequoian affinities. Our specimen differs, however, from *S. Penhallowii* not only in its lack of horizontal and vertical resin canals, but also in a greater abundance of wood parenchyma and lack of pitting in the tangential walls of the ray cells. Undoubtedly we are dealing with a transitional form between the old Abietinean stock and the present-day Sequoias, although, to be sure, the wood described here is much closer to the living *Sequoia* than their Abietinean ancestors.

Like most of our fossil forests the one at Florissant seems to have been rather badly neglected as regards detailed anatomical studies of the silicified stumps and trunks. It would seem that a study of the annual rings of some of the larger specimens might throw some light on the climatic conditions existing there during the Miocene.

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## EXPLANATION OF PLATE

## PLATE 20

*Sequoioxylon Pearsallii*, n. sp.

- Fig. 1. Photograph of the stump, Henderson Petrified Forest, Florissant, Colo.
- Fig. 2. Radial view of the strand tracheids.
- Fig. 3. Transverse section through two annual rings.
- Fig. 4. Tangential view of strand tracheids.
- Fig. 5. Tangential view showing tangential pitting in late summer tracheids.



1



2



3



4



5

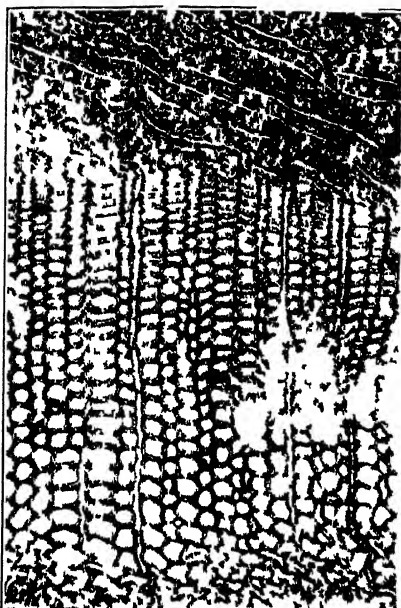


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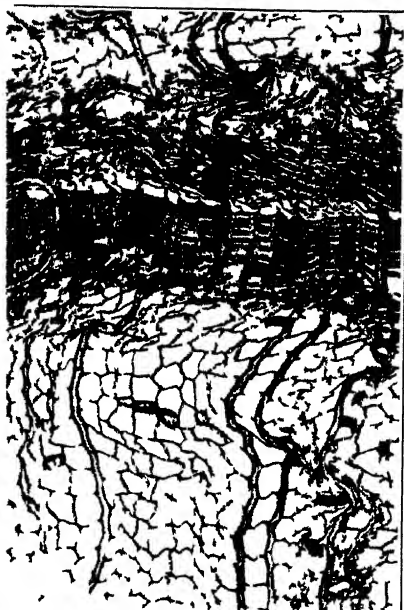
## PLATE 21

*Sequoioxylon Pearsallii*, n. sp.

- Fig. 6 Transverse section showing gradual transition  
Fig. 7 Transverse section showing abrupt transition  
Fig. 8 Strand tracheids in late summer wood  
Fig. 9 Portion of same more highly magnified



6



7



8



9



## FIELD AND HERBARIUM STUDIES, IV<sup>1</sup>

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***Picea pungens* (Parry) Engelm., Gard. Chron. N. S. 11: 334. 1879.**

During the past three preceding summers occasion was had to study the distribution of the Blue Spruce in Wyoming, of which there is probably a great deal more than is generally realized.

It extends, so far as was observed, along the Snake River, from Jackson Lake, in Teton County, at least to the Gorge of the river in Lincoln County, as well as up all of the tributary creeks and rivers. Along the Snake River, some fifty miles, it is the predominant conifer and is exceedingly abundant, but along the tributaries which usually gain elevation rather rapidly it is of less importance. In Sublette County it was found around Fremont Lake, Half Moon Lake, and other of the lakes in that vicinity. It is also to be found along the Green River but there it is not common. It does not ascend the river as far as the Green River Lakes; whether or not it goes farther down the river than a point due west of Pinedale is not known. The tree is also to be found, in this county, along the Hoback River which is a tributary of the Snake River. In Fremont County it was first observed near Dubois on the Wind River and extends up that river from there for several miles, and is also on some of the tributary streams. How generally it is distributed along the other creeks or how far it may extend down the east side of the Wind River Mountains remains to be investigated.

Acquaintance with the tree in Colorado does not quite give one an adequate idea of the species as it occurs in northwestern Wyoming. At first sight it may not be realized that it is the Blue Spruce. It is almost entirely lacking in any "blue cast." Again it is to be found only along the streams or at most no great distance from the water. The size attained is much

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greater than any the author has seen in Colorado. Trees four to five feet in diameter at shoulder height are not uncommon; one measured just under six feet in diameter. The height is in proportion.

The altitudinal limits seem to be rather definite. It is rarely found above 7500 feet altitude and so far as observed not below about 5700 feet. The best development is between 6000-7000 feet in Teton County. In this region the Blue Spruce is often associated with the Engelmann Spruce (*Picea Engelmannii* Parry). One tree, in such an association, observed above Dubois had cones which seemed to be intermediate both in size and in shape of the cone scales between the two species, but inclining slightly more toward those of the Blue Spruce. Cones observed from a tree on the grounds of the Lee Ranger Station, near Wilson, showed a large range of variation, particularly in shape of the cone scales but cones were not so small as on the tree near Dubois.

**Salix Tweedyi** (Bebb) Ball, Bot. Gaz. 40: 377. 1905.

This willow was found in abundance along Cascade Creek, one of the cold glacial streams in Grand Teton National Park. During the past summer it was found again in the Big Horn Mountains of Wyoming where the original collection was made. From Dr. Carleton R. Ball, who has kindly determined the material, comes the information that sets of this species have not been distributed among herbaria. My numbers 1133, 1668, and 1686 show it in various stages of development.

Specimens were collected in a spruce bog near Bald Mountain, elev. 9500 ft., Big Horn Co., Aug. 29, 1935, *Williams 2511*.

**Salix cascadiensis** Ckll., Muhlenbergia 3: 9. 1907.

This plant is quite common in Grand Teton National Park, between 9500 and 11,000 feet altitude, where it covers acres of ground. My numbers 915 and 1352, determined by Dr. Ball, illustrate it.

**Salix arctica** Pallas, Fl. Ross. I. 2: 86. 1784-1788.

This species is not mentioned in Rydberg's 'Flora of the Rocky Mountains and Adjacent Plains' or in the Coulter and

Nelson 'Manual of Rocky Mountain Botany.' It is found occasionally in Grand Teton National Park. My number 1708, determined by Dr. Ball, represents it.

**Populus taccamahacca** Miller, Gard. Dict. ed. 8. *Populus* No. 6. 1768.

Both the broad- and narrow-leaved forms are found in Teton County, Wyoming. The narrow-leaved form occurs along the streams in the valley. The broad-leaved form, which Dr. Alfred Rehder has kindly determined and which he informs me was not previously in the collection of the Arnold Arboretum from Wyoming, is to be found in the canyons of the Teton range.

**Xerophyllum tenax** (Pursh) Nutt., Gen. 1: 235. 1818.

This genus seems not to have been reported from the state of Wyoming. Two specimens are at hand, both sent to the author for determination and both from Teton County (slope north of Jackson Lake, July 11, 1932, *W. B. Sheppard*; four miles west of Cascade Creek on the road to Ashton, Idaho, along Reclamation Road, June 25, 1934, *Mrs. J. W. Orlob 1633b*).

Professor Nelson, in Coulter and Nelson's 'Manual of Rocky Mountain Botany,' p. 118. 1909, states the range as: "Montana, possibly Wyoming, and west to Oregon." In a letter he informs me that there are no specimens in the Rocky Mountain Herbarium collected in Wyoming.

**Paeonia Brownii** Dougl. in Hook., Fl. Bor. Am. 1: 27. 1829.

The published floras covering the Rocky Mountain region do not give this genus as occurring in Wyoming, yet several specimens from the northwestern part of the state have been in existence since 1860. More recently several collections have been made from the same area, of which the following may be cited: Jackson's Hole, on Snake River, June 18, 1860, *F. V. Hayden*; on Henry's Fork, June 19, 1860, *F. V. Hayden*; Lake Fork, June 22, 1860, *F. V. Hayden*; gravel flats, Jackson's Hole, Aug. 3, 1920, *Payson & Payson 2169*; near Jenny Lake, Grand Teton National Park, 1931, *Mrs. A. C. Lyon*; gravel flats near Jenny Lake, Sept. 2, 1933, *Williams 1434*.

The Hayden specimens were sent to Dr. Engelmann for determination but were not included in the published list of the plants of that expedition. They bear no annotations by Dr. Engelmann.

**Aquilegia Jonesii** Parry, *Am. Nat.* 8: 211. 1874.

This rare columbine was found again in the Big Horn Mountains. It seems to inhabit only the calcareous rock slides. My number 2358, July 5, 1935, represents it.

Roots and seeds were sent to the Cheyenne Horticultural Field Station at Cheyenne. It will be of interest to see if it survives in cultivation.

**Ranunculus jovis** A. Nels., *Bull. Torr. Bot. Club* 27: 261. 1900.

While the rocky flats of Grand Teton National Park were in most places still covered with two feet of snow and the temperature was below the freezing point each night this little plant was thriving. Indeed it had nearly matured its seed before the snow was gone from the flats. It is of interest to find this at an elevation as low as 7000 feet, since it is usually to be found in the alpine regions. (*Williams & Pierson 1074*, April 24, 1933, distributed as *R. glaberrimus* Hook.?).

**Thermopsis rhombifolia** (Nutt.) Rich., var. **annulocarpa** (A. Nels.), comb. nov.

*T. annulocarpa* A. Nels., *Bull. Torr. Bot. Club* 26: 239. 1899.

Professor Nelson in Coulter and Nelson's, 'Manual of Rocky Mountain Botany,' p. 271. 1909, referred this to *T. rhombifolia* as a synonym. However, it seems to merit varietal rank even though the characters by which it is distinguished are superficial. There seems to be another closely related variety of the species occurring on the western border of the range. Whether it represents an undescribed variety or is *T. arenosa* A. Nels. will have to await a study of the type of that species.

**Dalea Grayi** (Vail), comb. nov.

*D. laevigata* Gray, *Pl. Wright.* 2: 38. 1853, non Sesse & Moc. 1832.

*Parosela Grayi* Vail, *Bull. Torr. Bot. Club* 24: 14. 1897.

*Thornbera Grayi* Rydb., *N. Am. Fl.* 24: 119. 1920.

**Dalea Thompsonae** (Vail), comb. nov.

*Parosela Thompsonae* Vail, Bull. Torr. Bot. Club **24**: 18. 1897.

Among a fine collection of plants received from Mr. Bertrand Harrison for determination is a specimen which seems, *ex char.*, to be referable to this species. If the determination is correct it represents a considerable extension of range. The specimen bears the following data: dry sandy wash, excessively alkaline soil, Henry Mountains, Vanadium Mine, Garfield Co., Utah, May 20, 1934, *Harrison 7520*.

**Hoffmanseggia tenella** B. C. Tharp & L. O. Williams, n. sp.<sup>2</sup>

Slender perennial herb, 8–15 cm. tall; stem proper short, unbranched or nearly so, terminated by a few-flowered simple raceme; leaves bipinnate with 3–7 pinnae, as long as or exceeding the inflorescence, sparingly soft-pubescent, the petioles 5–13 cm. long; the pinnae with 5–6 pairs of pinnules, the pinnules sessile on the rachis or nearly so, 2–4 mm. long, 1–2 mm. broad, oblique, glabrous on the upper surface, sparingly pubescent on the lower surface and margins; stipules small, scarious, 1–2 mm. long, adnate to the petiole; inflorescence not exceeding the leaves, usually 3–5-flowered, each pedicel subtended by a short scarious bract; calyx about 4 mm. long, the lobes linear-oblong, obtuse, slightly naviculate, finely but densely pubescent; petals obovate, attenuated into a very short claw, 3–4 mm. long, 1.5–2 mm. wide; filaments free, with a few short hairs; mature legume 12–15 mm. long, 4–6 mm. wide, straight, finely and rather densely pubescent but not glandular; seeds 2–4.

TEXAS: Robstown to Alice, Nueces Co., Nov. 22, 1931, *Mrs. F. E. Clements 128b* (Herb. Univ. Texas, TYPE; fragment and photograph of type in Herb. Mo. Bot. Gard.).

This species seems to have its nearest ally in *H. drepanocarpa* Gray, from which it differs in several aspects. The

<sup>2</sup> *Hoffmanseggia tenella* B. C. Tharp & L. O. Williams, n. sp., herba perennis gracilis, 8–15 cm. alta, simplicia aut sparse ramosa; inflorescentiis paucifloris terminalibus; foliis bipinnatis, 3–7 pinnis, pubescentibus vel fere glabris, 5–6 paribus foliolarum; stipulis parvis, 1–2 mm. longis; calyce fere 4 mm. longo, pubescente, lobis lineari-oblongis; petalis obovatis, 3–4 mm. longis, 1.5–2 mm. latis; legumine 12–15 mm. longo, 4–6 mm. lato, recto, pubescente, sine glandulis.



leaves of the latter have 7–11 pinnae, those of ours have 3–7. In *H. drepanocarpa* the inflorescence usually exceeds the leaves and has several flowers, while in our plant it rarely if ever exceeds the leaves and the flowers are fewer. The legume of that species is 25–40 mm. long and is strongly falcate, while that of ours is about half or less that length and straight. Our plant is noticeably more slender than *H. drepanocarpa* and has fewer stems to the root.

**Dryas Drummondii** Richards., var. **tomentosa** (Farr), comb. nov.

*D. tomentosa* Farr, Ottawa Nat. 20: 110. 1906.

That this can be maintained as a distinct species on its rather meagre characters is doubtful. Juzepczuk, in Bull. Jard. Bot. URSS. 28: 311. 1929, places it in a new section, *Nothodryas*, of *Dryas*, along with *D. Drummondii* Richards. and *D. grandis* Juz. With the former, at least, it is closely related, but the latter has not been seen.

It is of interest to note that Juzepczuk, *l.c.* p. 325, describes a new species, *D. Hookerianum* from Rocky Mountain material. The writer is unable to find specific or even varietal differences between available material, which he cites, and European material of *D. octopetala* L.

**Zauschneria Garrettii** A. Nels., Proc. Biol. Soc. Wash. 20: 36. 1907.

*Z. latifolia* var. *Garrettii* Hilend, Am. Jour. Bot. 16: 66. 1929.

Finding this species above Bradley Lake in Grand Teton National Park came as a distinct surprise to the author. However, on looking up the distribution of the species several collections were found which were out of the range, "in mountains of Utah and southern Wyoming," given by Miss Hilend in her revision of the genus. The only specimen cited for Wyoming in that revision is from west-central, not southern, Wyoming. The following specimens may be cited:

WYOMING: hills east of Afton, Aug. 8, 1923, *Payson & Armstrong 3771*; ledges above Bradley Lake, Grand Teton National Park, Aug. 14, 1933, *Williams 1403*; mountains west of Cody,

Park Co., July, 1905, *Worthley*; mountain top, Holm Lodge, about 40 miles west of Cody, Aug. 26, 1922, *von Schrenk*.

***Rhododendron Warrenii*** Macbr., Contr. Gray Herb. N. S. No. 56, p. 55. 1918.

*Azaleastrum Warrenii* A. Nels., Bot. Gaz. 56: 67. 1913.

A consideration of the type and two subsequent collections of this species from Colorado, contained in the Rocky Mountain Herbarium and kindly loaned the author for study, raises a question concerning the taxonomic status of the species.

The collection on which the species is based is rather meagre; however, the description given for it is accurate. It compares very favorably with the abundant material at hand of *R. albiflorum* Hook., Fl. Bor. Am. 2: 43. 1834 (*Azaleastrum albiflorum* Rydb., Mem. N. Y. Bot. Gard. 1: 297. 1900), from the northwest in a similar stage of development.

An excellent collection, mountains due west of Walden, July 20, 1930, *Leonard Johnson*, from the same region, perhaps type locality, leaves little doubt that the plants are the same as those from the Northwest. The several hundred miles between the Colorado station and the nearest known station in Montana raises an interesting question in distribution.

Dr. Rydberg gave the distribution and range of *Azaleastrum Warrenii*, in the 'Fl. Ry. Mts. and Adj. Plains,' p. 640. 1917, as "Mountain slopes: Colorado." However, so far as it is known, it seems to occur only at the station at which it was first collected and near by, not nearly as widely distributed as Dr. Rydberg's note would indicate. The three specimens in the Rocky Mountain Herbarium are all from Jackson County.

***Nemophila petrophila* n. sp.<sup>3</sup>**

Low annual, 4–13 cm. tall; cotyledonary leaves persistent, opposite, obovate to oblanceolate, entire, 1–2 cm. long, 4–6 mm.

\* *Nemophila petrophila* n. sp., annua humilis 4–13 cm. alta; foliis cotyledonium oppositis, obovatis vel oblanceolatis, 1–2 cm. longis, 4–6 cm. latis, integris, infra glabris; foliis caulium ovatis, 1–2 cm. longis, pinnatis, lobis ovatis, integris, utrinque strigosis; floribus axillaribus; calyce fere ad basin diviso, lobis linearilanceolatis, 3–5 mm. longis, ciliatis; appendicibus in sinu 0.5–1.5 mm. longis; corolla fere 2 mm. longa.

broad, glabrous below, the petioles joined and sheathing the stem; cauline leaves opposite or rarely alternate, ovate in outline, 1–2 cm. long, 3–5-pinnate, the lobes ovate, entire, sparingly strigose on both surfaces; flowers usually one from the axils of the upper leaves; calyx 3 mm. long in flower, about 5 mm. long in fruit, divided almost to the base, the lobes linear-lanceolate, long-ciliate, otherwise glabrous or nearly so; reflexed appendages in the sinuses of the calyx lobes 0.5–1.5 mm. long, ciliate; corolla campanulate or apparently tubular, about 2 mm. long, shorter than the calyx-lobes, destitute of any appendages within, lobes ovate, about half of the length of the corolla; stamens attached near the base of the corolla by very slender filaments, barely reaching the orifice of the corolla; style 0.5–0.75 mm. long, enlarged and lobed at the apex but not divided; ovules two on each fleshy placenta, only one maturing; mature capsule round, 3–4 mm. in diameter, sparingly pubescent; seed round, 2.5–3 mm. in diameter, roughened or scarred at the apex, otherwise smooth, dull brick-red, solitary, filling the capsule.

WYOMING: rocky flats under *Pinus contorta*, Double Diamond Ranch, Grand Teton National Park, June 3, 1935, *Williams 2172*, TYPE; rocky open flats near Sensenbach's ranch, Grand Teton National Park, June 8, 1933, *Williams 1094*; Jackson's Hole, on Snake River, June 12, 1860, *Hayden*; marly soil, Jackson's Hole, June 14, 1860, *Hayden*; gravelly soil, Jackson's Hole, June 12, 1860, *Hayden*; rich marly hills, Jackson's Hole, in the valley of the Snake River, *Hayden*. All specimens cited in Herb. Mo. Bot. Gard.

This species seems to have its nearest allies in *N. parviflora* Dougl. and the closely related entities of that species as treated by Brand in 'Pflanzenreich,' Heft 59, IV. 251, pp. 54–55. 1913. It is quite common on the sagebrush flats in the region cited. The other species of the genus, *N. breviflora* Gray, which occurs in the mountains and in the same region as *N. petrophila* but along the moist swales and creek banks in the shade is quite distinct. Specimens of the proposed species were first collected by Hayden 76 years ago, but it seems not to have been found again until recently.

**Penstemon aridus** Rydb., Mem. N. Y. Bot. Gard. 1: 348. 1900.

Apparently the first known collections of this species for Wyoming were made by the author during the summer of 1935. Dr. F. W. Pennell, in his treatment of the genus (Contr. U. S. Nat. Herb. 20: 313–381. 1920), which covers Wyoming, did not include it. Rydberg in 'Fl. Ry. Mts. and Adj. Plains' gives the range as "Montana." The plant is quite abundant in the Big Horn Mountains. The two following collections are to be referred here: dry hillsides, lower Ten Sleep Canyon, Washakie Co., July 3, 1935, *Williams 2321*; dry western slopes of the Big Horn Mountains, ten miles east of Kane, Big Horn Co., July 5, 1935, *Williams 2348*.

**Penstemon Caryi** Pennell, Contr. U. S. Nat. Herb. 20: 354. 1920.

Excellent specimens of this rare species were secured in the Big Horn Mountains, where the type was collected. Dry western slopes of the Big Horn Mountains, ten miles east of Kane, Big Horn Co., July 5, 1935, *Williams 2349*.

**Pedicularis cystopteridifolia** Rydb., Mem. N. Y. Bot. Gard. 1: 365. 1900.

This rare and seldom collected species was found to be quite abundant in the Big Horn Mountains of Wyoming at elevations of 8000 feet and above, along the road between Dayton and Kane. In the field it shows a striking contrast to its near allies, *P. scopulorum* Gray, and *P. Hallii* Rydb. Number 2355 of my collections represents it.

**Downingia brachyantha** (Rydb.) Nels. & Macbr., Bot. Gaz. 55: 382. 1913.

Moist clay ditch banks, Evanston, Uinta Co., Wyoming, June 21, 1934, *Harrison & Larsen 7933*. This seems to represent the first reported collection of this genus for Wyoming.

**Microseris nigrescens** Henderson, Bull. Torr. Bot. Club 27: 348. 1900.

Dr. S. F. Blake, who has kindly determined my Compositae (except Senecio) collected during the past summer, informs me that this has been rarely collected. It is not uncommon in

moist meadows in the Big Horn Mountains and is represented by my number 2339, collected in moist meadows near Powder River Pass, Johnson Co., elev. 9000 ft., July 4, 1935.

**Senecio Harbourii** Rydb., Bull. Torr. Bot. Club **33**: 158. 1906.

Dry western slopes of the Big Horn Mountains, 10–15 miles east of Kane, Big Horn County, elev. 8000 ft., July 5, 1935, *Williams 2351*.

Dr. J. M. Greenman, who has kindly determined my *Senecios*, tells me that this seems to be the first recognized collection of this species in Wyoming. It extends the range of the species some 300 miles northward.

**Senecio spartioides** Torr. & Gray, var. **Fremontii** (Torr. & Gray) Greenman, comb. nov.

*Senecio filifolius* Nutt.  $\beta$  *Fremontii* Torr. & Gray, Fl. N. Am. **2**: 444. 1843.

Sandy hills near Hat Creek, Niobrara Co., Wyoming, *Williams s.n.*

This interesting variety of *S. spartioides*, although previously collected in Wyoming, seems not to have been reported hitherto for the state.

Specimens of all collections mentioned in this paper are to be found in the Herbarium of the Missouri Botanical Garden unless otherwise noted. Sets of my own collections have been or will be distributed to several American and European herbaria.

# THE SPECIES PROBLEM IN IRIS

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## I. INTRODUCTION

As a biological phenomenon the species problem is worthy of serious study as an end in itself, and not as a mere corollary to work in some other field. It is, to be sure, a problem so fundamentally important that it touches many such fields. Workers in any one of these are humanly prone to regard the evidence from that field as all important and its techniques as all sufficient (particularly if they are themselves unacquainted with other aspects of the problem). When, however, one takes up the problem, *as a problem*, and studies it from the diverse viewpoints of genetics, taxonomy, cytology, and biometry, he realizes that he not only needs most of the existing techniques but that he must devise new ones as well.

*Iris versicolor* and *Iris virginica* were chosen for such a study since they customarily grow in colonies containing many individual plants; a peculiarity which facilitates the location and study of large numbers of individuals. A preliminary analysis of the problem ('28) and a discussion of certain points connected with the distribution of these species ('33) have already appeared. The following series of papers constitutes a final comprehensive report. The central core of information is an analysis of a precise morphological census of the two species (section IV). For the interpretation of this morphological data it has been necessary to undertake correlated investigations in cytology, taxonomy, glacial geology, and genetics. A technical taxonomic treatment of these irises, together with the related *Iris setosa*, is assembled in section II, although material indirectly of taxonomic interest will be found in sections III and V. The phylogenetic relationship of *Iris versicolor* to *Iris virginica* has proved to be somewhat ex-

ceptional though it is by no means unique among the higher plants. The case has been presented in detail in section III as an example of reticulate relationship. Finally in section V the general problem of evolution in the genus *Iris* is discussed in the light of all the above information.

The major portion of these investigations has been carried out at the Missouri Botanical Garden and at the Arnold Arboretum of Harvard University. A fellowship from the National Research Council enabled me to acquire cytological and statistical techniques for continuing the work. During this time I was a guest of the John Innes Horticultural Institution and of the Rothamsted Experiment Station. A two-months' leave of absence from Harvard University in 1932 made it possible to study with Dr. Sewall Wright at the University of Chicago. Dr. Wright, Prof. J. B. S. Haldane, and Dr. R. A. Fisher have greatly furthered the final analysis of the data, though they are in no way responsible for the imperfections of the work or of its presentation. To the above individuals and institutions grateful acknowledgment is made for these exceptional opportunities. I am indebted to the University of Chicago Press and to Dr. J. Paul Goode for the base maps used in the second paper of this series and to Mr. Fred A. Barkley for figs. 2 and 13.

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- , ('33). The distribution of *Iris versicolor* in relation to the post-glacial Great Lakes. Rhodora 35: 154-160.

## II. THE TAXONOMY OF THE NORTHERN BLUE FLAGS

As a matter of convenience the essential facts in regard to the nomenclature, classification, and distribution of *Iris versicolor* and its relatives are summarized below. Such a segregation of the taxonomic aspects of the problem is essentially artificial and is dictated largely by practical considerations. Material of considerable taxonomic significance will be found throughout the other papers of this series. Attention is called in particular to pages 476 to 480, 495 to 496, and 501 to 506.

For the loan of material for study the author is indebted to the Curators of the following herbaria: Gray Herbarium, University of Wisconsin, Missouri Botanical Garden, United States National Herbarium, University of Pennsylvania, and the Canadian National Herbarium.

### KEY TO THE NORTHERN AND SUB-ARCTIC BLUE FLAGS

- A. Seeds with a conspicuous raphe; petals setose, less than 2 cm. long.
  - B. Stem short, usually unbranched; natives of eastern North America....  
.....*I. setosa* var. *canadensis*
  - BB. Stem various, often branched; natives of Asia and western North America.
    - C. Bracts often exceeded by the pedicels; stem usually branched; natives of central Alaska.....*I. setosa* var. *interior*
    - CC. Bracts exceeding the pedicels; natives of Asia and the northwestern coast of North America.....*I. setosa*
- AA. Seeds with an inconspicuous raphe or none; petals laminate, more than 2.5 cm. long.
  - B. Seeds D-shaped, sometimes with an inconspicuous raphe; surface of seed vernicose, regularly pitted; valves of the mature seed capsule reflexed but slightly, if at all; sepals minutely papillate at base of blade; outermost bracts of the inflorescence darker and somewhat vernicose along their margins.....*I. versicolor*
  - BB. Seeds round or D-shaped, without a raphe; surface of seed not vernicose, pitting irregular; valves of the mature seed capsule strongly reflexed; sepals macroscopically pubescent at base of blade; outermost bracts of the inflorescence with undifferentiated margins.
    - C. Seed capsules globose or subglobose; natives of the Atlantic seaboard.....*I. virginica*
    - CC. Seed capsules at least twice as long as broad; natives of the Mississippi Valley.....*I. virginica* var. *Shrevei*



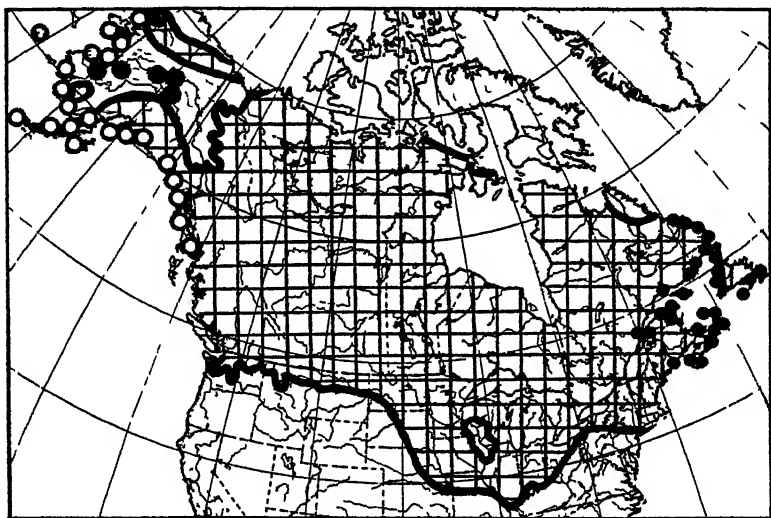
## IRIS SETOSA

*Iris setosa* Pall. ex Link in Spreng., Schrad. u. Link, Jahrb. d. Gewächskunde 1<sup>s</sup>: 71. 1820.

*Iris arctica* Eastwood in Bot. Gaz. 33: 132, fig. 2. 1902.

From coastal Alaska to the Lower Lena River and southwards to Japan.

Perennial from a superficial or underground rhizome; rhizome stout, thickly clothed with the fibrous remains of old leaves; leaves narrowly ensiform to linear, 9–65 cm. long, 0.5–



Map. 1. Range of *Iris setosa* (open circles), *I. setosa* var. *canadensis* (small solid circles), and *I. setosa* var. *interior* (large solid circles). Cross hatching shows extent of maximum Pleistocene glaciation.

1.7 cm. wide; stem slender to stout, 1–5 dm. high, unbranched or with one or two secondary branches, the latter *not exceeding the main axis*; upper cauline leaves *seldom equalling the inflorescence*; inflorescence a compact, 1–3-, mostly 2-, flowered fascicle; bracts of the inflorescence foliaceous to scarious, 3.5–8 cm. long; pedicels slender, exceeding the bracts or exceeded by them; sepals 4–6 cm. long; haft broad, the margin undulate; blade 3–5 cm. wide, *glabrous even at the base*, dark blue-violet (occasionally wine-colored) with *dark veins on a lighter ground-color*; petals small, *setose*; ovary short, 1–2 cm. long in

the flower, *conspicuously three-angled, inflated at anthesis*; capsule short-cylindric to ovate, *symmetrical, highly vernicose* within, often persisting on the plant for one or two years; seeds small, D-shaped, *with a conspicuous raphe, highly vernicose* over minute *regular pitting*; *chromosomes 38 (2n)*.

#### IRIS SETOSA VAR. CANADENSIS

*Iris setosa* Pall. var. *canadensis* Foster in *Rhodora* 5: 158. 1903.

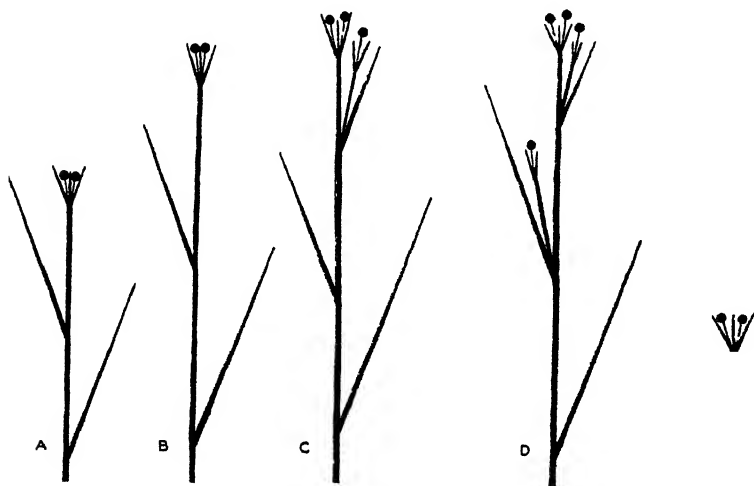


Fig. 1. Diagrams to scale of (a) *Iris setosa* from the Aleutian Islands and Alaskan peninsula; (b) *I. setosa* from northern coastal Alaska; (c) *I. setosa* from southern coastal Alaska; (d) *I. setosa* var. *interior*; (e) *I. setosa* var. *canadensis*. The diagrams are drawn to scale ( $\times 1/10$ ) from measurements and enumerations of the herbarium material. Each drawing represents average numbers and sizes for all the available material.

*Iris Hookeri* Penny in Steud. Nomencl. ed. 2, 1: 822. 1840.

From Labrador, around the Gulf of St. Lawrence; up the St. Lawrence River to Riviere du Loup, Quebec, and along the coast to Washington Co., Maine.

This typical preglacial relict differs from the type only in its generally smaller size and lesser variability. As was pointed out by Dykes,<sup>1</sup> the smallest of the Alaskan specimens are indistinguishable morphologically from *I. setosa* var. *canadensis*.

<sup>1</sup> Dykes, W. R., The genus *Iris*. p. 94. 1913.

The averages of the plants of the two regions are strikingly different, however, as can be seen from fig. 1. Its greater conservatism (i.e. its lesser variability) is a general characteristic of the relict species and varieties around the Gulf of the St. Lawrence, as has been pointed out by Fernald.<sup>2</sup> This point is discussed at greater length in another section of the paper (see below, pp. 495-496).

#### IRIS SETOSA VAR. INTERIOR

##### *Iris setosa* Pall. var. *interior*, var. nov.

Ab specie bracteis scariaceis vel crasse chartaceis non foliaceis rubicundiusculis saepe minoribus quam pedicellis differt.

Bracts scarious to thickly chartaceous, not foliaceous, somewhat florid, often exceeded by the pedicels.

Upper Yukon valley of Alaska, merging into the type in the lower valley and along the western coast.

ALASKA: Fort Gibbon, frequent throughout the Yukon and Tanana valleys in lakes and along small streams, July 4, 1905, *Heideman 62* (US TYPE); same locality, Aug. 10, 1905, *Heideman 98* (US); well-drained gully, Tolstoi, July 4, 1917, *Harrington 37* (US); Rampart, July 24, 1901 [fruit], *Jones 63* (US); alt. 150 m., vicinity of Fairbanks, Aug. 31, 1928 [fruit], *Mexia 2302* (MBG); Fairbanks, July 25, 1931, *Anderson 1221* (US); Fairbanks, June, 1927, *Palmer 1783* (US).

The characters which distinguish *Iris setosa* var. *interior* from the type have been found to characterize all the available herbarium material from interior Alaska. Transitional forms are to be found in the region where this great interior valley meets the coast. The following specimens represent such transitional forms:

ALASKA: Ft. St. Michaels, Norton Sound, 1865-66, *Bannister s.n.* (US); moist grassy places, shade of alders, 16 miles west of Nome City, Aug. 5, 1900 [fruit], *Flett 1560* (US); on the Yukon River, between Andreafski and Anvik, July 16-18, 1889, *Russell s.n.* (US).

According to glacial geologists,<sup>3</sup> this large region remained unglaciated during the Pleistocene, and there, if anywhere, we

<sup>2</sup> Fernald, M. L. Persistence of plants in unglaciated areas of boreal America. *Mem. Am. Acad. Arts & Sci.* 15: 244. 1925.

<sup>3</sup> Capps, S. R. Glaciation in Alaska. U. S. Dept. Inter., Geol. Surv. Prof. Paper 170-A. 1931.

might hope to find living irises most similar to those *Iris setosae* which must in preglacial times have extended across northern North America. A number of facts have been found which support this hypothesis and they are discussed below (p. 480).

While the irises of coastal Alaska are probably not varietally distinct from the type<sup>4</sup> (which is from Asia) there are minor geographical differences to be noted, when one compiles careful averages for such regions as the Arctic coast, the Alaskan peninsula and Aleutian Islands, and the southern Alaskan coast. Such averages have been prepared from all the available herbarium material and the results are presented graphically, to scale, in fig. 1, along with similar averages for *Iris setosa* var. *canadensis* and *Iris setosa* var. *interior*.

#### IRIS VERSICOLOR

***Iris versicolor*** L. Sp. Pl. ed. 1, 39. 1753.

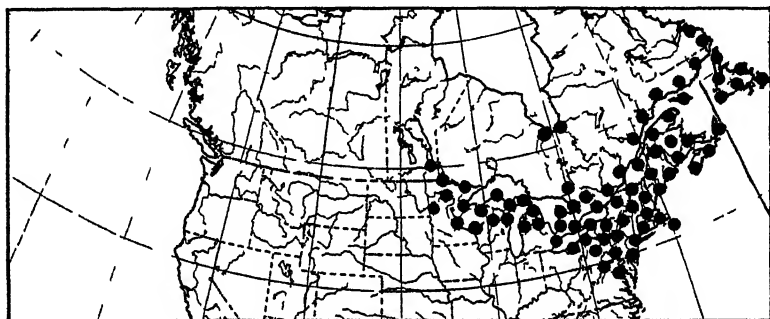
Perennial from a superficial or underground rhizome; rhizome stout, clothed with the fibrous remains of old leaves; leaves narrowly ensiform, 1-8 dm. long, 1-3 cm. wide, green to grayish-green; stem stout to slender, 2-6 dm. high, with one or two secondary branches, the latter *seldom equalling the main axis*; upper cauline leaves *seldom equalling the inflorescence*; inflorescence a compact, 2-4-flowered fascicle; bracts of the inflorescence thickly chartaceous to scarious, 3-6 cm. long, the margins *so heavily vernicose as to be much darker in color*; pedicels slender, some of those in each fascicle usually *longer than the subtending bracts*; sepals 4-7 cm. long, mostly *1.4 times the length of the petals* in living material; blade 2-4 cm. wide, variable in color in different plants, mostly violet-blue to blue-violet, the veins *slightly darker than the ground-color, minutely papillate at the base*, forming at most a dull greenish-yellow spot in living material; petals 2-5 cm. long, 0.5-2 cm. wide; ovary *1-2 cm. long in the flower, obscurely three-sided, slightly inflated at anthesis*; capsule short-cylindric, mostly symmetrical, somewhat verrucose without, *delicately vernicose*

<sup>4</sup>Hultén, Eric. Flora of Kamtchatka and the adjacent islands. Kungl. Svenska Vetenskapsakad. Handl. III. 5<sup>r</sup>: 255-256. 1927.

*within*, usually persisting into the first winter; seeds D-shaped, often showing a *poorly developed raphe*, surface *regularly pitted, vernicose*; *chromosomes 106–108 (2n)*.

From Labrador to Winnipeg and southward to central Wisconsin, northeastern Ohio, and northern Virginia.

Morphologically, *Iris versicolor* is much closer to *Iris virginica* than to *Iris setosa*, though in every character by which it differs from *Iris virginica* it departs in the direction of *Iris*



Map 2. Range of *Iris versicolor*.

*setosa*. This peculiar intermediacy is discussed at length in the following section of this paper (pp. 478–480).

#### IRIS VIRGINICA

*Iris virginica* L. Sp. Pl. ed. 1, 39. 1753.

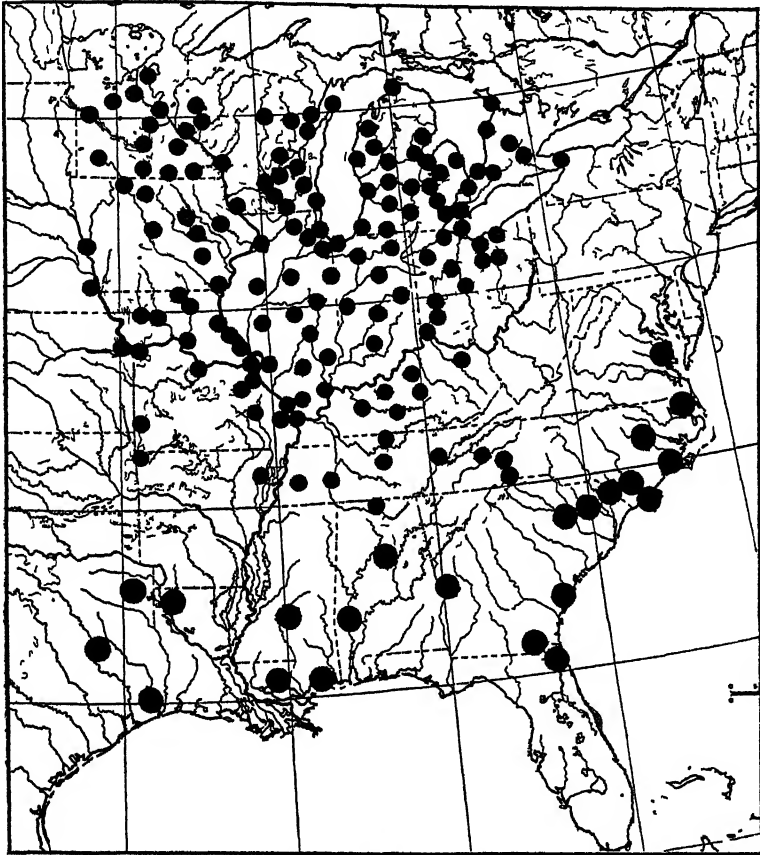
*Iris carolina* Radius, Naturforsch. Ges. Leipzig Schrift. 1: 158. pl. 3. 1822.

*Iris caroliniana* Wats. in Gray's Manual, ed. 6, 514. 1890.

*Iris georgiana* Britton, in Britton & Brown, Illust. Fl., ed. 2, 1: 537, pl. 1330. 1913.

Perennial from a superficial or underground rhizome; rhizome stout, clothed with the fibrous remains of old leaves; leaves ensiform, 2–9 dm. long, 1–6 cm. wide, green; stem stout, coarse, 3–10 dm. high, mostly with one secondary branch, the latter *usually subequal to the main axis*; upper cauline leaves *usually exceeding the inflorescence*; inflorescence a compact, 1–4-flowered fascicle; bracts of the inflorescence *coarsely* and

*thickly chartaceous*, 4–8 cm. long, *margins undifferentiated*; pedicels stout, *shorter than the bracts*; sepals 4–8 cm. long, mostly 1.2 times the length of the petals in living material; *haft narrow with a straight margin*; blade 1.5–4 cm. wide, blue to



Map 3. Range of *Iris virginica* (large circles), and of *I. virginica* var. *Shrevei* (small circles).

violet-blue and violet, veins scarcely darker than the ground-color, thick pubescence of fine hairs at base, forming a bright yellow signal patch in living specimens; petals 3–7 cm. long, 1–3 cm. wide; ovary 2–4 cm. long in the flower, terete or obscurely three-sided, not inflated; capsule spherical to long-

cylindric, mostly *asymmetrical*, *suberose* and *coarsely verrucose* without, *never verrucose* within, seldom persisting until the seeds are fully ripe, valves of the capsule reflexed in well-ripened specimens; seeds *round* or D-shaped, *without a trace of a raphe*, surface *suberose*, *irregularly pitted*; *chromosomes* 70-72 (2n).

From Virginia southward along the Atlantic coast.

Although well provided with distinguishing characteristics, *Iris versicolor* and *Iris virginica* seem to be under a special curse so far as their recognition in the herbarium is concerned. The shapes of the petals and sepals, the interior glandulosity of the calyx-tube and its shape—any one of these characters is sufficient for accurate specific delimitation. Unfortunately, *Iris virginica* differs also in texture and substance; its flowers, though larger, have less permanency. As a result they wilt very rapidly; even though carefully pressed when fresh, they have so little substance that the resulting specimens are too thin and fragile to be preserved intact. While the pressed flowers of *Iris versicolor* are none too accurate in their reflection of the original condition of the perianth, they are far superior to those of *Iris virginica*. The latter are so badly preserved that it is almost impossible to use them, even by boiling them up. Perianth dimensions from herbarium material are completely unreliable in these species, and for that reason have been largely omitted from the keys and descriptions.

The second most useful set of characters are those provided by the seed capsule and the seed. Here again the characteristic lack of permanency in the capsular walls of *Iris virginica* has been a great hindrance. With the exception of special collections made by the writer and by other recent students of American irises, herbarium specimens of *Iris virginica* seed capsules simply do not exist. The reason is not far to seek. The coarse stems of this species are neither durable nor stout, and they are not held above the leaves as in *Iris versicolor*. *Iris virginica* furthermore prefers slightly damper situations. In nature, therefore, the less lignified stems and seed-pods of *Iris virginica*, choked by iris leaves and other rank swamp vegeta-

tion, begin to rot long before the seeds are mature, particularly in the southern part of its range. By September it is not at all unusual to find the black, deliquescent, half-rotten seed-pods lying flat upon the ground, their corky brown seeds spilling out from the capsular remnants. A special collection of seeds and seed-pods has accordingly been brought together in the herbarium of the Missouri Botanical Garden as a permanent record, and the writer will be grateful for further material of either seeds or seed capsules, no matter how unattractive the partly decayed state of the latter.

It is unfortunate that mature capsular material is so difficult to obtain since it displays a curious and striking character, to which Small and Alexander<sup>5</sup> have called attention. The valves of the capsule in *Iris virginica* are strongly reflexed as in the related European species, *Iris pseudacorus* L.

Fortunately other characters can be found. Of these the most generally useful in the herbarium are the bracts of the inflorescence (the spathe-valves). Those of *Iris virginica* have the texture of coarse paper or thin cardboard. They may or may not be streaked with the fine chestnut lines caused by resinous deposits, but if so the streaking will be uniform throughout the bracts. In *Iris versicolor*, however, the bracts not only are of a finer, yet more durable texture, but the lignification is intensified towards the edge so that the margins are often deep chestnut and are distinctly vernicose.

In well-preserved specimens the pubescence at the base of the blade of the sepal is a useful character. In specimens of *Iris versicolor* it appears under the hand-lens as a minutely papillate area. In *Iris virginica* the hairs are larger, more overlapping, and are often conspicuously straw-colored.

In the field *Iris virginica* is readily identified by the larger, broader petals, the bright yellow pubescent spot on the sepal, and the spongy glandular inner surface of the calyx-tube with its sickish sweet fragrance.

Reasons for attaching the Linnean name *Iris virginica* to

<sup>5</sup> Small, J. K. and Alexander E. J. Botanical interpretation of the Iridaceous plants of the Gulf States. N. Y. Bot. Gard. Contr. 327: 356. 1931.



this species have been detailed elsewhere<sup>6</sup> and need not be repeated here, other than to state that the type is in existence and has been examined. The suggestion has since been made<sup>7</sup> that material from the presumable type locality may throw some doubt on this opinion. Through the kindness of Dr. T. W. Whitaker, I was able to obtain irises from Nesting, Gloucester County, Virginia, which is in the same general vicinity. Of these plants one or two answered the description given above; others showed signs of hybridization with *Iris versicolor* and were practically sterile. Reference to the distribution maps of *Iris versicolor* and *Iris virginica* (maps 2 and 3) will show that very region as the actual boundary zone of the two species. Because of this fact collections from or near the probable type locality are not so definitive as they otherwise might be.

*Iris virginica* is centered upon the Ozark-Appalachian land-mass, an area which has been available for continuous plant occupancy since very ancient times. It would be strange indeed if no geographical differences were to be found within such a species, particularly in the case of the area along the Atlantic seaboard. Such differences are, however, rather difficult to find. At flowering time, I have been able to detect for the plants of the Atlantic seaboard only slightly narrower perianth segments, a larger average flower size (fig. 12), and an inflorescence which is characteristically somewhat less branched. The seed capsules, however, though variable, are distinct. Well-developed capsules from the upper Mississippi Valley are much longer than broad, while those from the coastal plain are practically spherical, as well as possessing larger, corkier seeds. Unfortunately the difficulty of collecting fruiting specimens of iris in the southern swamps (see above, pages 466-467) makes exact delimitation of the areas occupied by these capsular types a matter of the future. Throughout the upper Mississippi Valley and Great Lakes region it has been a comparatively simple matter to determine, and I am accordingly

<sup>6</sup> Anderson, Edgar. The problem of species in the northern blue flag, *Iris versicolor* L. and *Iris virginica* L. Ann. Mo. Bot. Gard. 15: 241-332. 1928.

<sup>7</sup> Small and Alexander. loc. cit. p. 356.

using Dr. Small's name *Iris Shrevei* in a varietal sense for these elongate-capsuled *Iris virginicae*. When adequate material is available for study it will be possible to determine the exact geographical relationships of this and probable other varieties of *Iris virginica*. Until such a time it has seemed prudent to recognize only this one variety, and to postpone for the present the precise delimitation of the typical and other possible varieties.

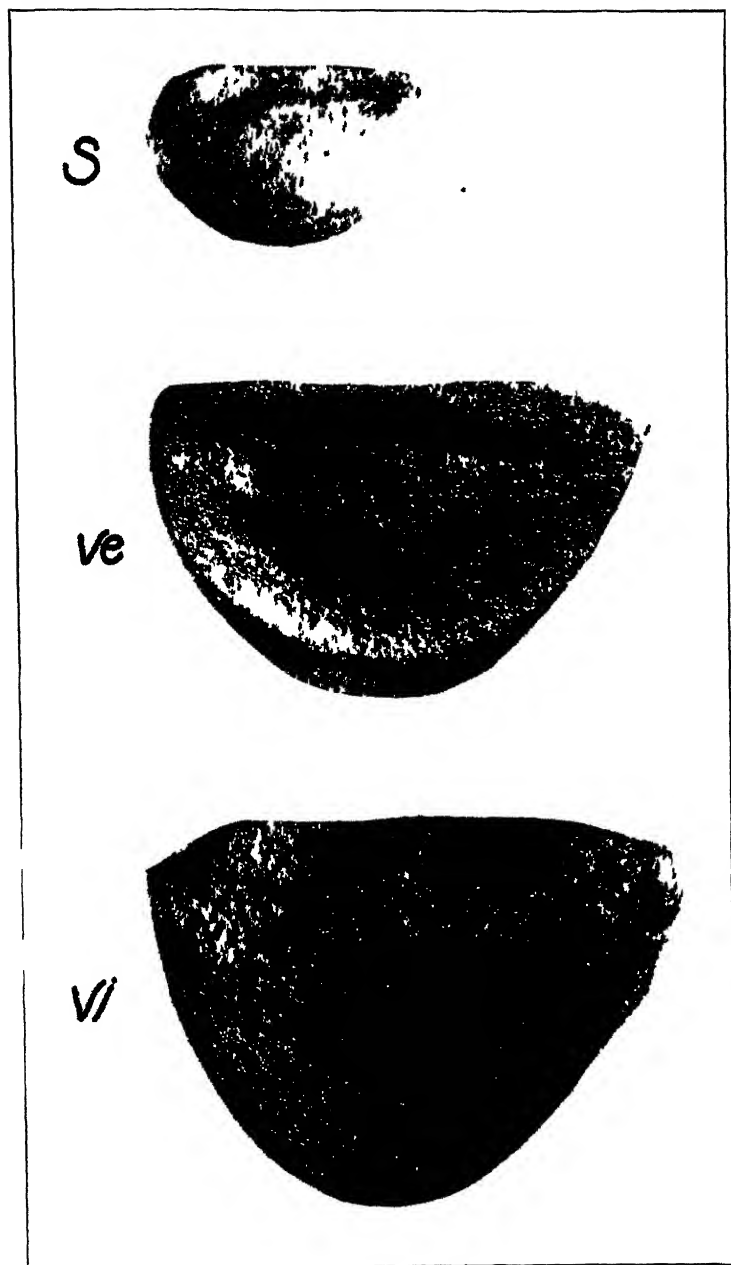
IRIS VIRGINICA VAR. SHREVEI

***Iris virginica* L. var. *Shrevei* (Small), comb. nov.**

*Iris Shrevei* Small, *Addisonia* 12: 13-14, pl. 391. 1927.

Mississippi Valley and Great Lakes region from southern Minnesota and southern Ontario, southwards to Texas and Alabama. The exact boundaries of its junction with the type as yet unknown and perhaps complex.





Seeds  $\times 10$ : s, *Ilex sclosa*; ve, *I. viscolor*; vi, *I. virginica* var. *Shrevei*.



### III. THE PHYLOGENETIC RELATIONSHIP OF *IRIS VERSICOLOR* AND *IRIS VIRGINICA*

The northern blue flags, *Iris versicolor* and *Iris virginica*, were originally chosen for study because they were known to be closely related and preliminary investigation had shown that in any one locality they varied markedly from plant to plant. It was accordingly planned to study the minutae of variation so intensively in these two species that one might demonstrate the way in which one species had evolved from the other, or from some common ancestor. It seemed at the beginning of the work that here was splendid material for illustrating the way in which individual differences merge into racial, racial into varietal, and varietal into specific. A confident beginning was made with this end in view: five years of hard work showed that *Iris versicolor* might vary greatly and that *Iris virginica* might vary greatly but that each remained itself. They were of different fabrics. One might compare them to two old English villages, one in a sandstone region and the other in limestone. In each village there would be no two houses alike but all the houses in one village would be made of limestone, all those in the other made of sandstone. The conclusion was reached that closely related though these irises might be, variation within either species was of quite another order of magnitude from the hiatus between them (Anderson, '28). The variation *within* could never be compounded into the variation *between*. The two species were made of two different materials.

If one of these species was *not* derived from the other through the slow accumulation of minor differences, in what other manner could it have originated? Fortunately, at about the same time that these detailed studies of variation came to an *impasse* there were published a number of accounts dealing with another way in which species might originate in the higher plants: amphidiploidy. This phenomenon may well be illustrated by the case of *Primula kewensis* (Newton and Pellew, '29). *Primula kewensis* originated as a highly sterile hybrid between *P. floribunda* and *P. verticillata* (fig. 2). Kept alive by

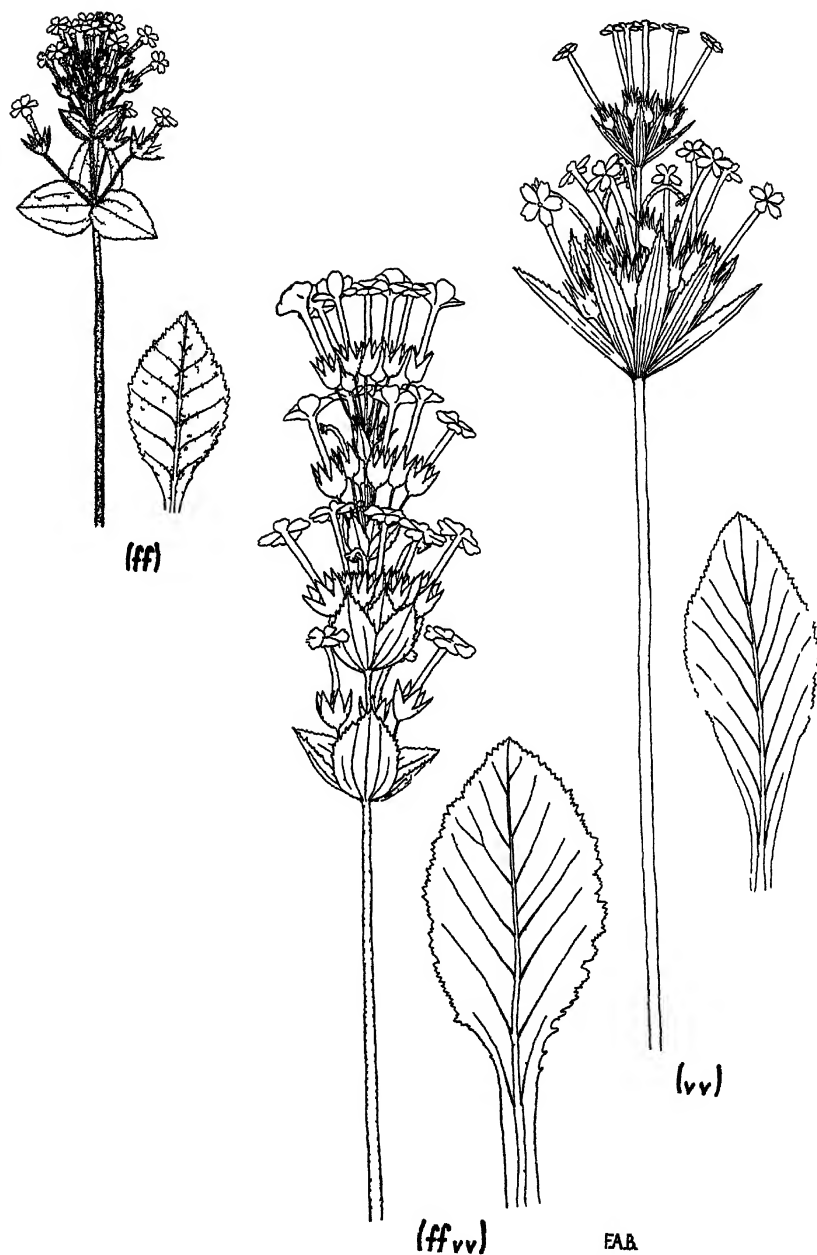


Fig. 2. *Primula floribunda* (ff), *P. verticillata* (vv), and then amphidiploid hybrid *P. kewensis* (ffvv). Drawn from herbarium specimens collected in the greenhouses of the John Innes Horticultural Institution

vegetative reproduction, it has on several occasions produced fertile flowers. The progeny from these exceptional flowers have furthermore bred true, or substantially so, and the hybrids are today grown commercially by means of this fertile strain. Cytological examination has demonstrated that this fertile, true-breeding hybrid has 18 pairs of chromosomes, while the sterile hybrid and each of the parental species has 9 pairs. The fertile hybrid evidently originated when an exceptional nuclear division in the inflorescence of the sterile hybrid was not accompanied by a cell division and a sector arose in which the entire chromosome complement had been duplicated. On this hypothesis *Primula floribunda* might be diagrammed as  $9F + 9F$ ; *P. verticillata* as  $9V + 9V$ ; the sterile hybrid as  $9V + 9F$ ; and the fertile hybrid as  $9V + 9V + 9F + 9F$ . The original hybrid was sterile because the two sets of chromosomes (V and F) were too unlike to pair and produce fertile gametes. Doubling the number resulted in two sets of V's and two sets of F's so that pairing could proceed regularly, producing a fertile, true-breeding hybrid, or amphidiploid.

Amphidiploidy, the production of fertile, true-breeding hybrids by doubling of the chromosome number, is now known to be a fairly common phenomenon among the higher plants (Winge, '32). It has occurred under controlled conditions in the experimental plots of many investigators. More than 24 such cases are now on record including several among floristically indigenous species (Müntzing, '30, '32; Clausen, '33). It has apparently occurred in the development of the cultivated irises (Randolph, '34). Amphidiploidy is largely confined to the flowering plants and is foremost among several factors which make specific relationships among the higher plants more intricate and more various than they are among the higher animals (Anderson, '31).

If our two blue flags did not originate by the slow accumulation of individual differences, the most likely explanation of their fundamental divergence is that one or both of them came into existence suddenly through amphidiploidy. A simple hypothesis immediately suggested itself.



*Iris versicolor* is geographically and morphologically intermediate between *Iris virginica* and the Arctic blue flag, *Iris setosa*. Might it be possible that *Iris versicolor* is an amphidiploid hybrid between these two species, a hybrid which occurred in pre-glacial or inter-glacial time? Startling as such an hypothesis seemed, it found confirmation in facts from such diverse fields as geographical distribution, cytology, morphology, and genetics. The hypothesis was used, with complete success, to predict the presence in central Alaska of a previously unrecognized variety of *Iris setosa*. It orients a number of facts which are either puzzling or meaningless on any other hypothesis. For all practical purposes it may be taken as proved though it is capable of still further tests.

The facts which support this hypothesis may be grouped under several different heads:

1. *Genetics*.—Although they have been placed in different sub-sections of the genus, *Iris virginica* and *Iris setosa* are at least partially fertile *inter se*. It is difficult in this latitude to bring both species into flower at the same time, but on one occasion it was possible to do so and two pollinations were made. From these two crosses of *Iris virginica*  $\times$  *Iris setosa* were obtained two seed-pods well-filled with seeds, but with shrunken endosperms. None of them germinated, but it seems likely that if the cross could be repeated in quantity a few viable seeds could be obtained. It should be pointed out in passing that the most successful amphidiploids so far obtained have been between plants which are ordinarily quite sterile with one another. As was first pointed out by Darlington ('28, pp. 244-245), the more inter-sterile the two parents of an amphidiploid, the more fertile and true-breeding is the resulting progeny.

2. *Cytology*.—The cytological investigation has been hampered by the high chromosome numbers of *Iris virginica* and *Iris versicolor*, the highest known in the genus. This makes the determination of chromosome number and configuration rather difficult, and I am happy to report that my own counts have been completely confirmed by several other investigators,

principally by Randolph ('34). *Iris virginica* has 70 to 72 chromosomes [2n], *Iris setosa* has 38, and *Iris versicolor* has just what we would expect if it is an amphidiploid hybrid of the

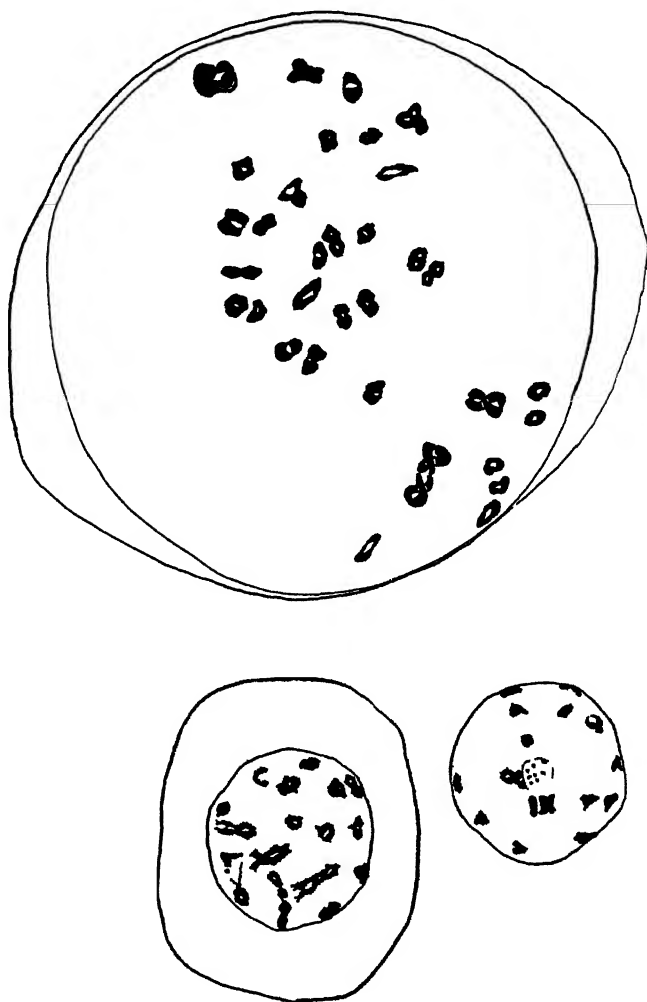


Fig. 3. Above: smear of early metaphase PMC. of *Iris virginica* var. *Shrevei* from Frankenmuth, Michigan, somewhat distorted by pressure. Camera-lucida drawing (made at bench level at  $\times 2280$ , reduced to  $\times 1140$ ).

Below: smear of PMC. of *Iris virginica* var. *Shrevei* from Frankenmuth, Michigan. Late diakinesis, upper and lower hemispheres drawn separately.

two, 108 chromosomes. *Iris virginica* shows occasional multivalent association, mainly in fours, and very strong secondary association (fig. 3). These facts would suggest that it is itself an ancient amphidiploid hybrid of two species each with  $36\pm$  chromosomes. *Iris versicolor* has occasional multivalents; hexavalents such as the one illustrated in fig. 4 are not uncommon. The cytological facts therefore are in complete agreement with our hypothesis, and they go even farther by suggesting that *Iris virginica* is a set of two genomes and *Iris versicolor* the component of three genomes.



Fig. 4. Aceto-carmin smear of PMC. of *Iris versicolor* from Connecticut Lakes, N. H. Camera-lucida drawing (made at bench level  $\times 2280$ , reduced to  $\times 1140$ ).

3. *Geographical evidence.*—The three species of irises which we are considering have strikingly different distributions in North America, and the distribution of each is characteristic of many of the plants with which it is found. The significance of these areas has been pointed out by Fernald ('31). Of the region about which the *Iris virginica* is centered he says: "Temperate eastern North America has, then, an extensive area (the southern Appalachian Upland) in which land-plants have had an opportunity to spread since the advent of the Angiosperms."

The other putative parent species, *Iris setosa*, also comes from a region (again we quote Fernald) "which apparently retained [its] present distinctive flora through at least the last glaciation."

*Iris versicolor*, which we are presuming to derive from these two ancient species, inhabits a more youthful region, one characterized by Fernald (loc. cit., p. 28) as "the vast region of Canada and the Northern States which has become available for wholesale occupation by plants only since the decay of the Wisconsin ice, within the last few thousand years."

The geographical facts, therefore, point to *Iris virginica* as an ancient southern species and to *Iris setosa* and its variety *canadensis* as being certainly pre-glacial. *Iris versicolor*, our putative hybrid, is either late pre-glacial or inter-glacial. The present distributions of the species would suggest that the original hybridization (or hybridizations) took place in the interior of the continent, perhaps in the general region of the present-day Great Lakes. As will be shown below there are morphological reasons for believing that the *Iris setosa* which entered into the cross was not the depauperate remnant which lingered on around the Gulf of St. Lawrence. The actual ancestor is rather to be sought among the hordes of *Iris setosa* which must have occupied the interior of the continent before the glacial period.

4. *Habitat*.—In its habitat preferences *Iris versicolor* is likewise intermediate. It grows in situations more moist than those preferred by *Iris setosa* and a little drier than those in which *Iris virginica* is found. The three species are not found growing together in nature at the present time but *Iris versicolor* is found with each of the others. Around the Gulf of St. Lawrence the marked preference of *Iris setosa* var. *canadensis* for drier situations has been noted by a number of investigators. In Michigan and Ontario, where *Iris versicolor* and *Iris virginica* are growing together, it can be seen that *Iris versicolor* will continue to flower and fruit in spots so dry that *Iris virginica* only persists vegetatively. It is not uncommon to find *Iris virginica* growing luxuriantly in marshes where

there is standing water over its roots for several months during the growing season. *Iris versicolor* may tolerate such a situation but does not welcome it.

5. *Morphology*.—Before considering these data in detail it may be well to point out again that, according to our hypothesis, *Iris versicolor* was formed by the summation of *Iris setosa* with 38 chromosomes and *Iris virginica* with 70. In other words it received two doses of *Iris virginica* but only one of *Iris setosa*. We should expect therefore to find *Iris versicolor* in an intermediate position morphologically but much closer to *Iris virginica* than to *Iris setosa*. Such does actually prove to be the case.

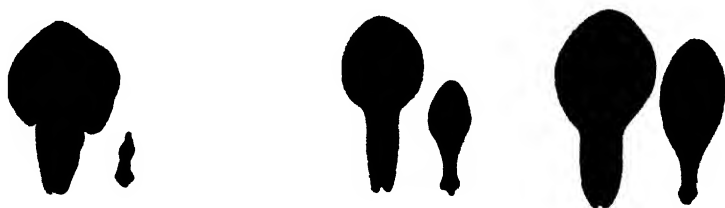
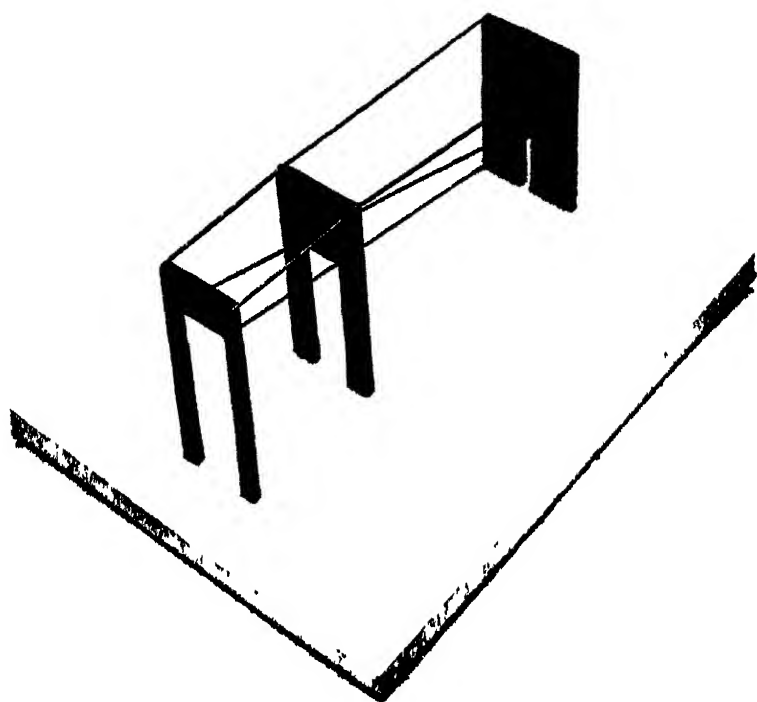


Fig. 5. Outline drawings of petal and sepal from plants of *Iris setosa* (left), *I. versicolor* (center), and *I. virginica* var. *Shrevei* (right).

In the living plant the size and dimensions of the petals and sepals are among the best diagnostic characters for these three species (as indeed for most species of *Iris*.) It will be seen that *Iris setosa* differs from *Iris virginica* in having a shorter, broader sepal and a much smaller and narrower petal. *Iris versicolor*, as our hypothesis demands, has differences in this direction. These significant dimensions are presented diagrammatically in fig. 5. These differences in proportion of sepal and petal are so absolutely in accord with the theoretical demands that, given any two of the three species, it is possible to derive the average proportions of the other by statistical prediction (pl. 23).

The sepals of *Iris virginica* bear a bright yellow pubescent patch, the hairs of which are clearly visible to the naked eye. No such patch exists in *Iris setosa*, and the epidermal cells are



Photograph of three-dimensional model showing the precise geometrical relationship in petal and sepal size and proportions of *Iris virginica* (left), *I. versicolor* (center), and *I. setosa* (right). In the model, *Iris versicolor* is placed two-thirds of the distance between the two putative parents, since their chromosomal contributions to the hybrid are in the approximate ratio of 2 to 1. Measurements combined by method illustrated in figure 8.



seen to be barely papillate when examined with a strong hand-lens. *Iris versicolor* is intermediate; the bearding is clearly visible only with a hand-lens and the color is at best a kind of greenish-yellow. The blade of the sepal in *Iris setosa* is broad and slightly undulate, in *Iris virginica* it is narrow and straight; *Iris versicolor* presents an intermediate condition.

The ovary of *Iris setosa* inflates rapidly after fertilization so that in the ripening capsule there is a wide space between the walls and the seeds. In *Iris virginica* the walls are stretched tightly over the seeds, in *Iris versicolor* the condition is intermediate though nearer to that of *Iris virginica*.

In *Iris setosa* the capsules and stem are so strongly lignified that they sometimes persist for over two years, and it is customary to find last year's seed stalks among this year's flowers. In *Iris virginica* the capsule and stem, though much larger, are poorly lignified. In the humid swamps of the south they fall over and the capsule usually is more or less disintegrated by the time the seed is ripe. Here again *Iris versicolor* is intermediate; the capsules usually persist well into the winter but are seldom found the second season.

*Iris setosa* bears seeds which are unique in the genus. They are small, heavily vernicose, and with a conspicuous raphe down one side. *Iris virginica* bears large, spongy seeds which may be either round or D-shaped. When the above working hypothesis was first considered, one possible objection seemed to be the fact that *Iris versicolor* was without a raphe. Subsequent examination of the seeds of *Iris versicolor* shows that it does have the shadow of one on nearly every seed and had even been illustrated as having one (though without comment) in Dykes' plate of *Iris* seeds in his monograph of the genus ('13). (See pl. 22.)

When minute comparisons were made in this way, character by character it was found that there were, however, at least three characters in which *Iris versicolor* was not intermediate between *Iris virginica* and *Iris setosa* var. *canadensis*. The theory demanded an *Iris setosa* with several flowering branches, with pedicels longer than the bracts, and with bracts not greenish but brown and subscarios. Since the demands of



the theory were met so minutely on all the other characters it seemed possible that these three represented details in which the race of *Iris setosa* entering into the original hybridization differed from *Iris setosa* var. *canadensis*. Such a race might conceivably have present-day relatives living among the *Iris setosa* which is so widely spread in Alaska and Asia, since the species is notoriously variable there. Herbarium material was accordingly consulted. The first few specimens examined proved most disappointing. They were from localities along the arctic coast and they had none of the three desired qualities. Their bracts were long and green, completely eclipsing the pedicels, and the plants were unbranched. Farther down in the pile, however, was a plant which had not only long pedicels, but scarious bracts and a branched inflorescence, the very combination desired. Farther on was another and eight specimens in all were found.

When their distribution was plotted it was found that all came from central interior Alaska and represented, in fact, the only specimens from that region. They have accordingly been described above in the taxonomic section of these papers as a new variety, *Iris setosa* var. *interior*.

Further search unearthed the even more significant fact that *Iris setosa* var. *interior* grows in that part of Alaska which was adjacent to the edge of the continental ice-sheet (map 1). If representatives of the pre-glacial races of *Iris setosa* which must once have covered much of northern Canada are to be sought anywhere today, glacial geologists would suggest this very region (Capps, '31). In other words, we not only found the variety demanded by the theory but we found it in exactly the region which the theory would suggest as most likely.

The comparison of the three species can be closed therefore with the presentation of diagrams to scale of *Iris virginica*, *Iris versicolor*, and *Iris setosa* var. *interior*. It will be seen that in size, node number, leaf length, number of branches, length of pedicels, and length of bracts the demands of the hypothesis are exactly met (fig. 6).

Though it is capable of still more rigorous tests, the theory that *Iris versicolor* is a pre-glacial, or inter-glacial, amphi-

diploid hybrid between *Iris virginica* and *Iris setosa* var. *interior* would seem to be well established as a working hypothesis. Ultimately it should be possible, as in the case of the European *Galeopsis Tetrahit* (Müntzing, '30), to re-synthesize the species from its two constituents.

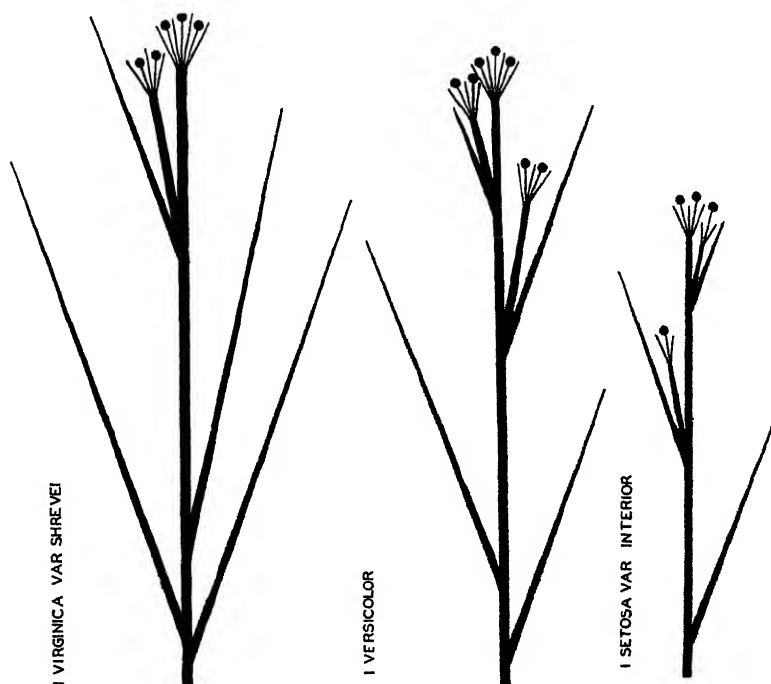


Fig. 6. Diagrams to scale of *Iris setosa* var. *interior*, *I. versicolor*, and *I. virginica* var. *Shrevei*. The diagrams represent precise averages of all the available herbarium material.

The hypothesis also gives an explanation to several curious facts which had previously been most puzzling. The first might be called the one-way relationship between *Iris virginica* and *Iris versicolor*, or so I have attempted to phrase an impression received from long-continued study of variation within these two species. It seemed that the relation of *Iris versicolor* to *Iris virginica* was quite different from that of *Iris virginica* to *Iris versicolor*, or to state it somewhat less mystically, that *Iris versicolor* often reminded one of *Iris virginica*, but *Iris vir-*

*ginica* never reminded one of *Iris versicolor*. If on the above hypothesis *Iris versicolor* is indeed *Iris virginica* plus something else, then the relationship should be different in one direction from what it is in the other.

Another puzzling fact had been the frequency of albinos. *Iris virginica* and *Iris versicolor* by any ordinary standard were unusually variable species yet pure albinos were exceedingly rare. In spite of prolonged search and inquiry I found only three in *Iris virginica* while in *Iris versicolor* I have found no pure albino without a trace of blue, and only one case has been reported in the literature (Fernald, '36). Yet albinos are common in many species of *Iris*, as, for instance in *Iris missouriensis*; why then should they be absent from our common blue flags? Why should they shun this particular species which by any other standard is peculiarly variable in flower color? On the above hypothesis this is exactly what one might predict. If *Iris virginica* is made up by the summation of two ancient species, albinism, being recessive, cannot appear until it has occurred in each of the constituent sets. In *Iris versicolor* it cannot show itself until it appears in these and also in the set of chromosomes derived from *Iris setosa*. This means that if the original frequency of albinism in the basic species had been, say one in every 5000, that we should find it in *Iris virginica* once in every 25,000,000 and in *Iris versicolor* only once in 125,000,000,000. The infrequency of albinism in *Iris virginica* and its even greater rarity in *Iris versicolor* is therefore in strict accord with theoretical expectations.

#### SUMMARY

1. The absolute morphological discontinuity previously discovered between the closely related *Iris versicolor* and *Iris virginica* is explained by the following hypothesis: *Iris versicolor* originated suddenly as a fertile, true-breeding hybrid (an amphidiploid) between the southern *Iris virginica* and the subarctic *Iris setosa*, in pre-glacial or inter-glacial times.

2. Since the former has 70 chromosomes and the latter 38 we should expect to find *Iris versicolor* generally intermediate be-

tween these species though much closer to *Iris virginica*. This is found to be the case.

3. A consideration of one or two minor exceptions to this generalization led to the discovery of a previously unrecognized variety from central Alaska, *Iris setosa* var. *interior*.

4. Since it harmonizes so many otherwise incoherent facts from cytology, morphology, geographical distribution, genetics, and geology, the theory is taken to be well established as a working hypothesis.

5. The theory also explains two phenomena which had previously seemed incomprehensible: (1) the "one-way" morphological relationship between *Iris virginica* and *Iris versicolor*, (2) the infrequency of albinos in *Iris virginica* and their even greater rarity in *Iris versicolor*, a species otherwise unusually variable in flower color. It is shown that both of these results are to be expected on the basis of the above hypothesis.

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#### IV. INTRA-SPECIFIC DIFFERENTIATION IN THE NORTHERN BLUE FLAGS

As has been related in the previous paper of this series, detailed studies of variation were made in two species of *Iris* with the aim of demonstrating the way in which one had arisen from the other. Though they failed to produce any such evidence (and have as a matter of fact led to a very different hypothesis of the phylogenetic relationship between these two particular species), the data may still be used to examine the way in which evolution has proceeded and is proceeding to build up differences within these species. Many of the actual data have been presented in full in a previous communication (Anderson, '28). Since that time, however, the interpretation of this evidence has been profoundly affected by information derived from other fields of study.

The following paper is largely concerned with the results of a detailed morphological census of two species of *Iris* in eastern North America, *I. versicolor* and *I. virginica*; some attention has also been paid to the related glacial relict, *Iris setosa* var. *canadensis*. The results of such a census may be presented individual by individual or they may be grouped and averaged in various ways. In the following census the colony is recognized as a vegetational and evolutionary unit of major importance, so far as irises are concerned. Throughout most of the region in which they are found today, *I. versicolor* and *I. virginica* grow in small colonies of from one to several thousand individuals. Single individuals usually cover several square feet and send up several flowering stalks each year. In exceptional cases one individual may by vegetative reproduction cover a much larger area, and in rare instances a colony of several acres may be composed genetically of but one plant.

With a little study the recognition of individual plants is not at all difficult. The sea of blue-purple flowers which at first glance seems so uniform resolves itself into a little community with quite as much divergence between the various members as is found in human communities. One plant will have brown spots on the sepals of each flower, the next one will be without

the spots but will claim attention by the extraordinary size of its petals. Another will have flowers which are a very light blue, still another will have flowers which are almost wine colored, another will have deep notches in the petals. And just as in a village each man has a hand with characteristically different proportions from all other men yet has his left and right hands built on almost the same pattern, so it is in a swamp full of irises. The petals and sepals of the different flowers on a plant will have substantially the same proportions, but these proportions will vary tremendously from plant to plant. This point is illustrated in pl. 24 where three flowers are shown from each of six plants. These photographs were taken with identical illumination and exposure and were developed and printed uniformly. The differences in shade are due to differences in the flowers themselves; plant no. 2 had flowers of a very light blue and they have photographed almost white; plant no 6 had a great deal of red in with the blue and it is much darker in the picture. It will be noticed that even such a tenuous character as the carriage of the petals and sepals is based upon inherent factors; note, for instance, the floppy aspect of all three flowers of no 5, the contrasted horizontal sepals and upright petals of no. 1, the undulate sepal margins of no. 3.

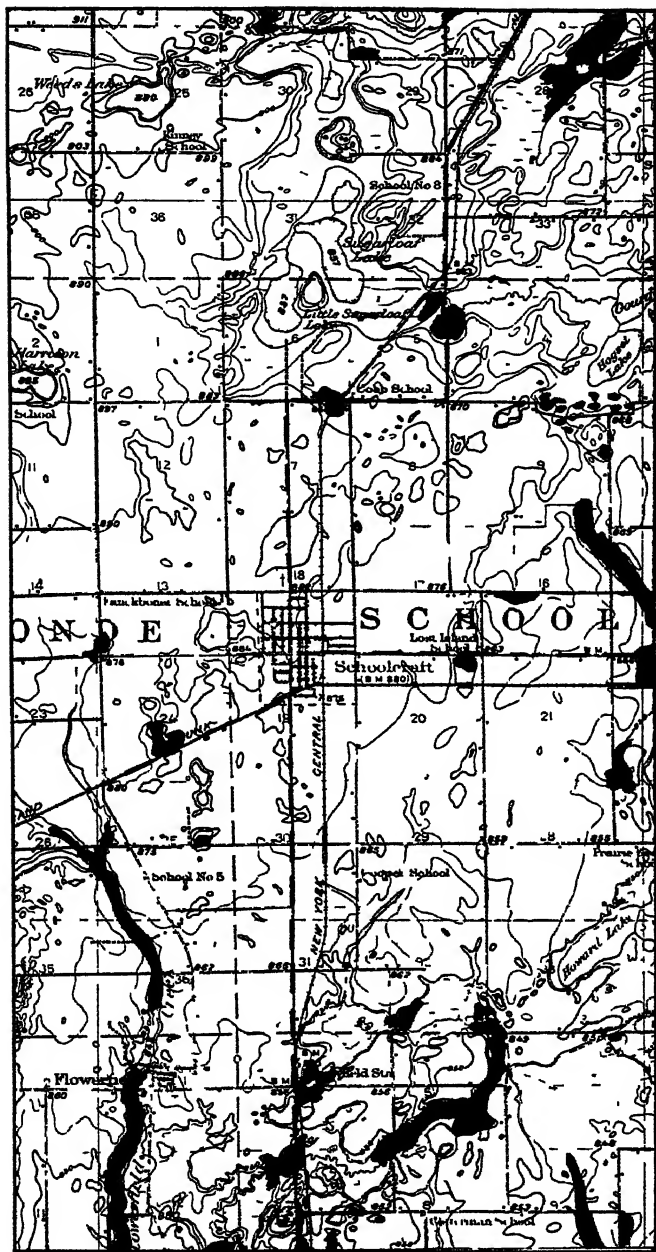
The number of such colonies is enormous; a rough approximation has been made by observing the numbers to be seen from the highway along various routes and converting these figures into number of colonies per square mile. The method seems to be reasonably accurate, since it yields consistent results when different trips are made through the same territory. According to this method, the average frequency of *Iris* colonies per 100 square miles is 120 in northern Michigan, 350 in southern Michigan, 170 in northern Illinois, 30 in southern Missouri, and 5 in Alabama and Mississippi. Colonies are particularly frequent north of the terminal moraine where an uneven glacial topography produces many small swampy areas favorable for the growth of *Iris*. Figure 7 illustrates a representative area of 50 square miles within this region. It



Three flowers each from six plants of *Iris virginica* var. *Shriver* from Portage des Sioux, Missouri







demonstrates how numerous are the *Iris* colonies and how isolated they are from one another.

It is a point of some theoretical importance (see below, pp. 495—496) that the colonies are probably distributed in much the same way that they were before the land was cleared but that

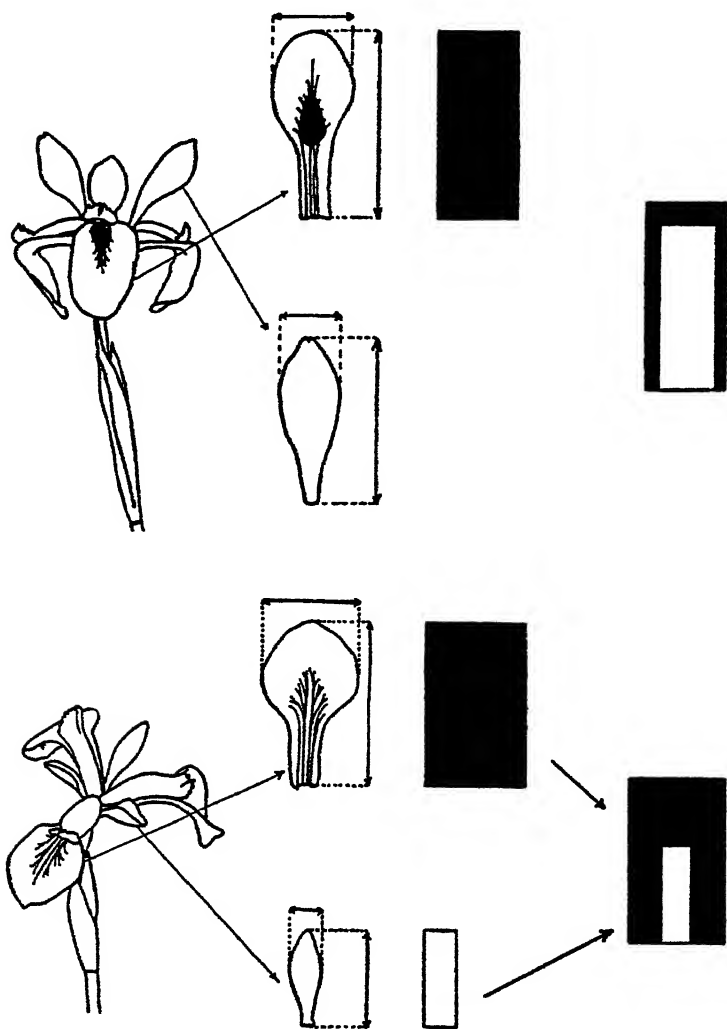


Fig. 8. Diagram illustrating how petal length and width, and sepal length and width are combined to form an ideograph. Above, *Iris virginica*; below, *I. versicolor*.

the numbers of individuals in the colonies are greater. The deforestation and pasturing of swampy areas have increased many fold the area available for these irises throughout the northern states. Turning the land over to pasture is particularly helpful to them since grass, their worst competitor, is kept down by the livestock. In most cases large colonies now numbering thousands of plants are probably the descendants of a much smaller number which were growing in that area before the land was cleared.

The census has to do with four measurements; length and width of sepal, length and width of petal. Since such measurements are of greatest significance when their interrelations with each other are understood, the results are presented graphically in a way which makes it possible to convey these relationships simultaneously. Figure 8 shows how the four measurements of each flower can be built up into a simple black-and-white diagram. This diagram or "ideograph" is essentially a white petal superposed upon a diagrammatic black sepal. Figure 9 presents ideographs for 20 plants of *Iris versicolor* and 20 of *Iris setosa* var. *canadensis* which were growing together in a pasture near Île Verte, Quebec (Anderson, '35). It demonstrates how such ideographs may be used to present a large amount of data in a small space. Figure 9 is a graphical summary of four measurements and six proportions on each of 40 plants. It is, in other words, a simultaneous presentation of 400 separate facts. The precise comparison of such colonies can be carried farther by the production of *average* ideographs for the whole colony, utilizing the average petal length, the average petal width, the average sepal length, and average sepal width (fig. 9, central ideographs).

The data for colonies are presented in this way in figs. 10 and 11. The colonies are arranged by species and subspecies and within these categories are placed roughly according to geographical position from south to north. A study of these figures yields the following conclusions:

1. There is little or no regional differentiation in shape within any of the subspecies. No general characteristics can be recognized for the irises from southern Michigan or from

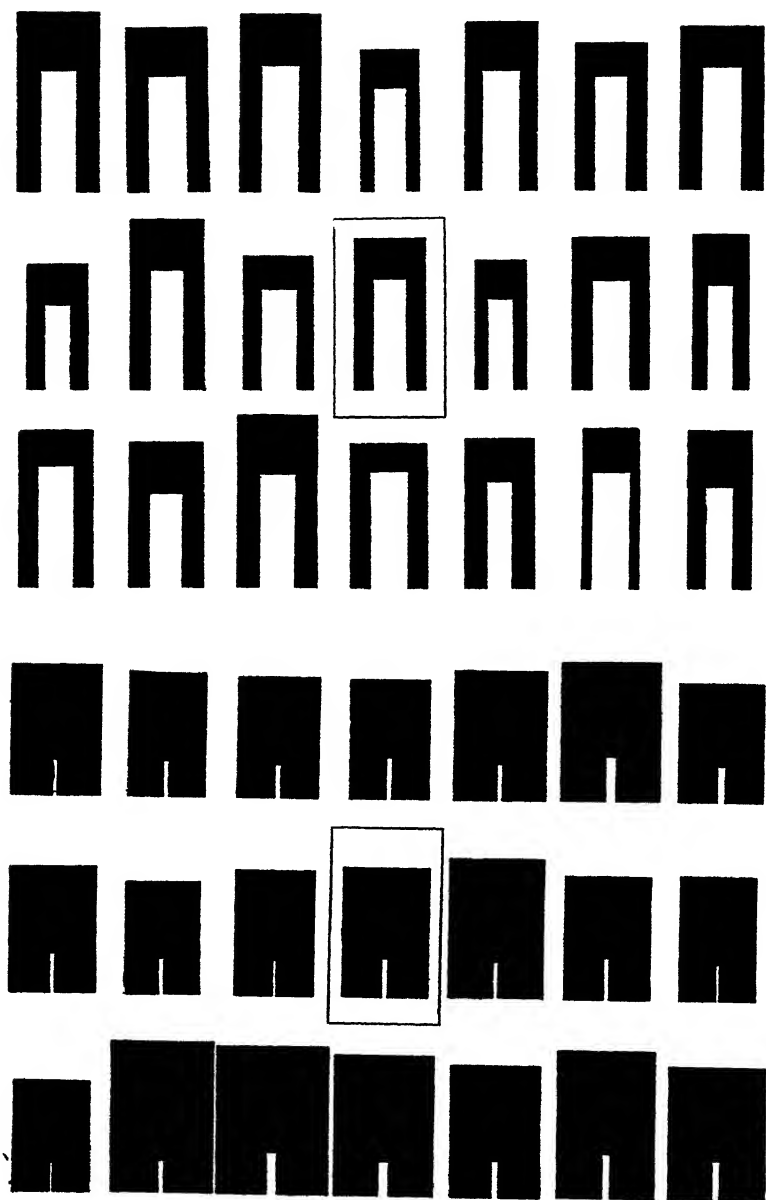


Fig. 9. Ideographs of 20 plants of *Iris versicolor* and 20 of *I. setosa* var. *canadensis* from Ile Verte, Quebec. Averages of entire colony (50 for each species) shown in central frames.

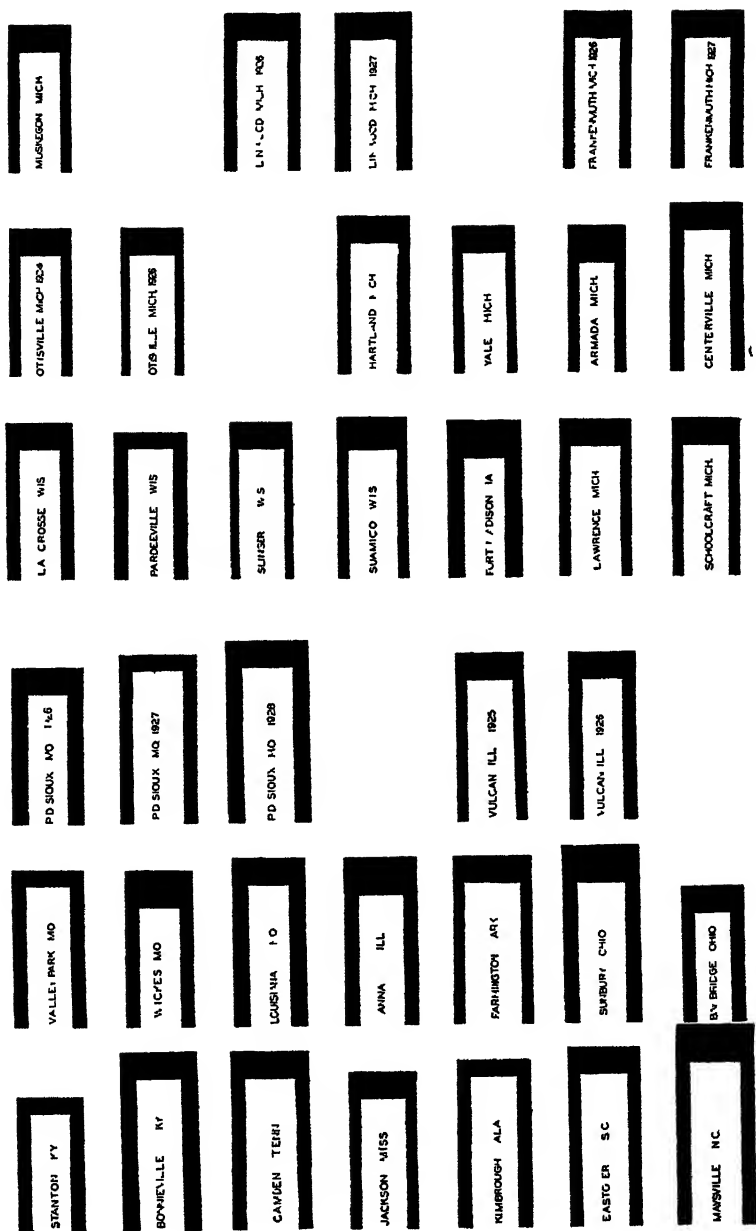


Fig. 10. Average ideographs for 31 colonies of *Iris virginica* and *I. virginica* var. *Shrevei*.

the Mississippi Valley, or from the Cumberlands, or from the prairies. As will be shown below, this conclusion is reinforced by the computation of *regional* averages.

2. There is a very slight trend in size. *Iris virginica* var. *Shrevei* reaches its greatest development in the Cumberlands of Kentucky and Tennessee. Northward or southward it becomes somewhat smaller on the average. *Iris versicolor*, on the contrary, is largest in the north and becomes smaller



Fig. 11. Average ideographs for 18 colonies of *Iris versicolor*.

towards its southern limits. Transplants from these various areas have kept their same relative sizes when grown together in the experimental garden.

3. Colony averages are fairly consistent from year to year in those cases where measurements could be made in different years. Allied to this fact is the experimental evidence that the flowers of plants collected and grown together in the garden maintained their characteristic size, shape, color, and color pattern. In several cases divisions of the same plant have been grown and studied in Boston, St. Louis, and Schoolcraft,

Michigan. For these reasons the differences which distinguish the individual plants and thereby create the peculiarities of the colonies are thought to be largely inherent. An even stronger proof is the fact that progeny tests of several individuals produced evidence for the heritability of various individual peculiarities.

4. There are striking differences between colony averages, even for the same region. The colony averages of figs. 10 and

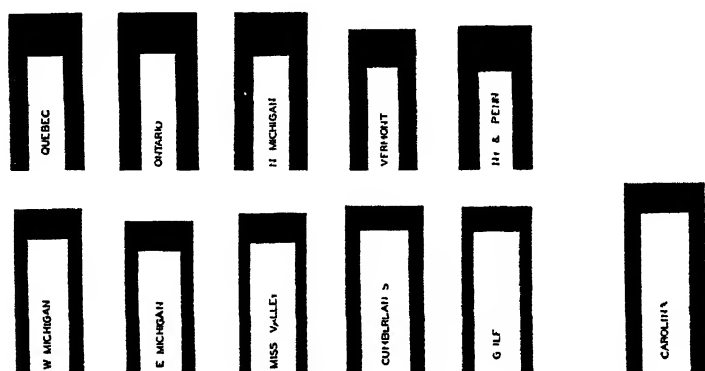


Fig. 12. Regional averages for *Iris versicolor* (above), *I. virginica* var. *Shrevei* (below, left) and *I. virginica* (below, right).

11 are particularly instructive when compared with the regional averages of fig. 12. It will be noted that though there are differences between the regions they are slight, and they have no evident geographical trend other than the slight one in size already referred to. The regional differences are indeed so slight that the variation in these irises might seem to be without any phylogenetic significance. If attention is shifted from the regions to the colonies, the evolutionary significance of the variation is more manifest. Each little colony is a more or less independent evolutionary unit and has evolved a more or less distinctive combination of characters. All that is necessary for the production of a regional variety is the isolation of any *one* of these colonies. Were some succession of droughts and floods to exterminate the great bulk of either species, leaving only two or three colonies persisting in different parts of



its present range, and were the area to be repopulated from these centers we should then have the formation of geographical varieties. The majority of the colonies as they exist at the present have achieved sufficient individuality to be rated as incipient varieties were they only to reproduce their several types over larger areas. For an actual difference of this magnitude we may compare *Iris virginica* of the Atlantic seaboard and *Iris virginica* var. *Shrevei* of the Mississippi Valley. For an inconceivably long time the irises of the seaboard have been somewhat isolated from their relatives in the Mississippi Valley. It is not surprising then that though we can find no outstanding differences in sepal and petal proportion within the interior of the continent, there is a slight difference between the irises from the interior and those from the seaboard. *Iris virginica* has flowers which are distinctly larger and somewhat narrower. The difference is a minor one as compared to the distinct hiatus between *I. versicolor* and *I. virginica*, but it is reinforced when we study such technical characters as the shape of the seed capsules and the size of the seed.

Particularly significant is the fact that the difference between *I. virginica* and *I. virginica* var. *Shrevei* is of about the same order of magnitude as the differences between colonies of *I. virginica* var. *Shrevei*. It would indeed be possible to find two swamps in the same township in southern Michigan whose iris populations have as great an average difference as that between *Iris virginica* of the Atlantic Coastal plain and *Iris virginica* var. *Shrevei*. But in this latter case the difference, slight though it is, characterizes a whole region and has superimposed upon it the varying pattern of colony differences in each region.

An evolutionary factor of basic importance in our common blue flags, therefore, is the rapid accumulation of minor differences in the little colonies into which the species are divided. Nearly every colony carries within itself the potentialities of a variety or a subspecies. The conditions under which these irises exist seldom release these potentialities. Many colonies arise, develop a distinctive type, and pass on with little or no influence on the main evolutionary stream. It should be re-

membered that the territory in which they are growing possesses very few geographical or climatic barriers. But the potentiality is there and when opportunity allows a colony to play a larger role it is ready to do so. Then the peculiarities evolved in one colony, or a few colonies, might come to characterize all the colonies of a region.

By mathematical deduction from the known facts of genetics, Wright ('31) has produced a generalized theory of evolution. From the standpoint of pure theory he finds that evolution will proceed most effectively neither in a large inter-breeding population nor in a very small one but in a large population "divided and sub-divided into partially isolated local races of small size." Under such conditions he predicts "a continually shifting differentiation among the latter which inevitably brings about an indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species."

The irises of this study present just such a picture. They are divided into partially isolated small colonies ["Local races"] which before the land was cleared were probably even smaller. These colonies differ from one another and from the mean of the species to a degree which is almost of varietal magnitude. Their differences are inherent and to all appearances are largely non-adaptive. Isolation, in dividing the species up into these smaller units, has made possible their several divergencies. Were isolation to be made complete, as by another glacial period, the phylogenetic potentialities of the survivors would be released and what had been colonial peculiarities might become varietal differences.

The variation within *Iris setosa* var. *canadensis* seems particularly instructive in the light of its recent history. It is typical of those species whose once continuous range across northern North America was reduced to the northeastern and northwestern edges of the continent by the Pleistocene ice. In Alaska a large central region was left unglaciated; around the Gulf of St. Lawrence, on the other hand, the plant refuges in glacial times were little more than rocky nunatacks rising above the ice. The results on the two sets of irises are just what a geneticist might predict. Even from the few specimens

which are available in herbaria one can see that the *Iris setosae* of Alaska are a varied assemblage. They include one well-marked variety (described above) and several fairly well-marked regional variants. The irises of eastern Canada present a very different picture. Figure 9 gives some slight indication of their lesser variability from plant to plant. Compared to the millions of irises which might well have continued to live in Alaska during the ice age, those of the St. Lawrence region were a mere handful. From that handful must have descended the millions upon millions of irises which now carpet the meadows and shores of that region in early summer (Anderson, '35). Compared with our other American blue flags they are a singularly invariable lot. Graphical comparisons are made in fig. 9. They are furthermore the smallest, much smaller than any other recognizable type of *Iris setosa* (note fig. 1). They are short, seldom branching, with small leaves and few nodes.

This conservatism of *Iris setosa* var. *canadensis* is distinctive of most of the glacial endemics (or near endemics) of the region around the Gulf of St. Lawrence. In one of his classic contributions to the subject, Fernald ('29) has aptly characterized them as "already waning types, too old, or too conservative to spread into closely adjacent and virgin soils." In the case of *Iris setosa* var. *canadensis* the invariability cannot be a direct effect of time, for the highly variable irises of Alaska are quite as aged. It is more probably, as Professor Fernald has suggested, an innate conservatism; a conservatism founded genetically upon the fact that these irises are descendants of a small and highly selected stock. Hard times removed from the region all the luxuriant types which may once have existed there. When the ice age was over the immediate area was repopled from the few plucky survivors. Their descendants, *Iris setosa* var. *canadensis*, bear the scars of the glacial period, so to speak, in their conservatism; an innate invariability which, on the one hand, gives them a greater uniformity, and on the other, prevents their adapting themselves readily to other environments.

In the light of its probable history, it is not surprising to find

no regional differentiation in *Iris versicolor*. If, as seems probable, it originated in interglacial times, it is a comparatively young species. It is furthermore inhabiting a region which is extremely youthful floristically, most of it not becoming available for plant occupancy until the last retreat of the Pleistocene ice. Having only recently moved into most of the territory it now occupies, *Iris versicolor* has had as yet little or no opportunity to develop geographical races within the species.

Much the same argument can be made for the northern flank of *Iris virginica* var. *Shrevei*. It is in this part of its range, thanks to irregular glacial topography, that it occurs most frequently and is therefore most easily studied. Within this area there is little or no evidence of geographical races. Were it possible to study *Iris virginica* and *Iris virginica* var. *Shrevei* in the same detailed manner on the older lands they occupy in the south, it is more than probable that considerable geographical variation would be found. There are indications of such differentiation in the few samples from these areas which are available in herbaria. A detailed statistical census would probably reveal still more.

#### SUMMARY

1. Most of the northern blue flags occur in more or less isolated colonies of from a few to many thousand individuals. The average frequency of such colonies per 100 square miles was found to vary from 350 in southern Michigan to 5 in Alabama and Mississippi.

2. From a statistical study of 60 colonies it is shown that there is little regional differentiation within any of the subspecies. Even within the same region, however, there are pronounced differences between the colonies.

3. The colony is an important evolutionary unit in these irises. Through its isolation each colony develops a distinctive type which is of potential phylogenetic importance.

4. It is shown that the differences between geographical varieties in these irises are of about the same order as differences between colonies. Many of the colonies carry the po-

tentialities of a variety or a subspecies, though these are seldom released by the conditions under which they exist.

5. The conservatism of *Iris setosa* var. *canadensis* is discussed in the light of its history as a glacial relict. Its comparative invariability and poor colonizing ability are probably innate as suggested by Fernald. They result genetically from the fact that this subspecies has descended from what in glacial times must have been a small population living under adverse conditions.

6. The lack of geographical differentiation within *Iris versicolor* and the northern colonies of *Iris virginica* var. *Shrevei* is correlated with their occupancy of a floristically youthful territory. *Iris virginica* var. *Shrevei* would probably reveal greater regional differences if it could be studied on floristically older lands in the south.

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## V. THE EVOLUTIONARY PATTERNS OF THE GENUS *IRIS*

Students of the species problem are faced with a curious dilemma. By the nature of that problem they are forced to confine their attention to the details of a few species; yet if they do so exclusively they will be unable to interpret their results in general terms. The details of evolution vary from genus to genus and even from species to species; when one discusses the evolutionary patterns discerned by intensive work on one or two species he must attempt to determine to what extent those patterns are general characteristics of most species and to what extent they are special features of those few. Throughout the following discussion an attempt will be made to apply the information derived from these three species of *Iris* to the entire genus. It is as yet too early to consider the larger problem of speciation in the higher plants in the light of these results, except in the most general way.

In addition to the correction factor for the peculiarities of the germ-plasm one must also allow for the peculiarities of the region in which the studies were made. Speciation is a function of the region under observation. If a region is without pronounced barriers, speciation for most of the organisms in that area will be simpler than in an area with a complex system of barriers and partial barriers. It will also be affected by the age of the region. In one floristically young, geographical differentiation within species will be less intense than in regions which have been continuously available for occupancy for a long period of time. It should therefore be kept in mind during the following discussion that these studies were, for the most part, carried on in an exceedingly youthful region floristically and one in which there are no geographical barriers of any great importance.

A number of processes of evolutionary significance are taking place in these irises, all of which affect the ground-plan of the genus. Three of them, hybridization, amphidiploidy, and colonial differentiation, have produced effects which were readily perceptible by the methods used in this study. A general summary of the results is presented graphically in fig. 13.

The fundamental pattern is composed of the three species, which can be represented as great compound cables, stretched from the past into the future. For long eras these cables are practically parallel; even the detailed methods of this investigation have produced little or no evidence for the ultimate derivation of these separate cables from a common source.

Examining these cables more closely it is apparent that they are made up of smaller cords, the colonies. These cords likewise maintain their individuality for considerable time. Such a division of the species into small colonial units is probably characteristic not only of these three species but of a good part of the genus *Iris*. Certainly the other species with which I am personally acquainted in the field, *I. fulva*, *I. foliosa*, *I. prismatica*, *I. foetidissima*, *I. pseudacorus*, and *I. missouriensis*, grow in much the same sort of more or less isolated colonies.

Within this small group of irises there are three apparent cases where colonial differences have developed into geographical varieties. Very anciently the *Iris virginicae* of the Atlantic seaboard became slightly differentiated from those of the Mississippi Valley. As has been shown above, this difference is of about the same order of magnitude as that between colonies and is therefore most easily interpreted as due to some ancient geographical change which reduced one or both of these regions to one or a few colonies. By some such process also *Iris setosa* var. *interior* diverged from the *Iris setosae* of coastal Alaska and of northeastern Asia. More recently, during glacial times, *Iris setosa* var. *canadensis* was reduced to a highly inbred remnant (see pp. 495-496).

At the present time, therefore, *Iris virginica* is composed of two slightly divergent sub-cables, *Iris setosa* of three, and the youthful *Iris versicolor* is as yet but a single cable. Supposedly by the successive compounding of such divergencies, subspecific differences might be built up into differences of specific magnitude. There is little evidence in this study to contradict such a theory, but it should be pointed out that there is none to support it. In the opinion of the author the theory that geographical varieties are potential species is a debatable one.

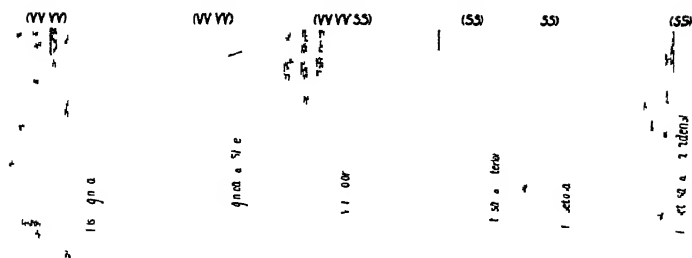


Fig. 13. Diagram showing phylogenetic relationships in the northern blue flags. Further discussion in the text.





Observation and experiment have shown (Anderson, '28) that in *Iris versicolor* and *Iris virginica* the colonies themselves are more or less divided into inbred lines, so that in these species we can speak of the colony "cords" as being made up of pure-line "threads." Since cross-pollination occurs occasionally the threads maintain their identity for only a few generations. This detail of the evolutionary pattern will vary greatly from *Iris* species to *Iris* species. There are very probably species in which inbreeding is more severe; there are certainly self-sterile species in which there is complete outcrossing. In the former the threads would be longer, in the latter there would be no recognizable threads at all within the colony cords (Anderson, loc. cit. pp. 308-310).

The great ground pattern of the cables is a simple one, with two exceptions. Very occasionally by amphidiploidy a single strand runs out from one trunk line to another and at an intermediate point a whole new cable arises. An earlier paper of this series presented detailed evidence for the amphidiploid origin of *Iris versicolor*. The secondary pairing and multiple association characteristic of the pollen mother-cells of *Iris virginica* strongly suggest that it is itself the result of an ancient amphidiploid hybridization, perhaps between a species somewhat like *Iris tripetala* and one related to *Iris hexagona*.

Such occasional interweaving of phylogenetic lines is apparently characteristic of most of the genus *Iris*. Simonet ('34) reports chromosome numbers for the section Pogoniris which suggest amphidiploidic relationships and has presented cytological proof ('35) for the occurrence of amphidiploidy in cultivated irises. As Randolph has shown (loc. cit., p. 65), there is experimental evidence that in *Iris*, species with differing chromosome numbers cross more readily than in many other genera. He also presents some evidence for the functioning of unreduced gametes in *Iris*. Both of these conditions favor amphidiploidy. The presence of even occasional amphidiploidy within a genus will so complicate the phylogenetic relationships that it will be impossible to divide and subdivide it naturally into sections and subsections. We would therefore predict for the genus *Iris* that while there might be evidence of

groups of related species, it would be impossible to arrange all these groups in a clear-cut natural system. Such is actually the case. The latest monographer of the genus has the following to say about the difficulties of subdividing the section *Apogon*, numbering some 50–100 species and native to Europe, Asia, and North America: "It seems unfortunately impossible to select any one character or set of characters to form a guide through the maze of species. . . . The classification given below is therefore admittedly unsatisfactory partly because some of the species seem to stand by themselves and to have little or no affinity to any others" [Dykes, '13]. He then proceeds to divide the section into fifteen sub-groups. On the theory outlined above *Iris versicolor* is an amphidiploid hybrid between *Iris virginica* of his group X and *Iris setosa* of group XIV. A few relationships of this sort would produce exactly the difficulties which Dykes describes.

The other tangle in the evolutionary pattern of these irises is provided by hybridization. Though such tangles are a characteristic feature of the evolutionary pattern in the genus *Iris*, they form in this group of species a small knot of minor consequence. *Iris virginica* and *Iris setosa* are now geographically isolated, though they still in part occupy the same river system. *Iris setosa* var. *canadensis* and *Iris versicolor* grow together throughout the range of the former, but there is very great numerical isolation between them (38 vs. 108 chromosomes). Hybrids are occasionally found, but they are very rare. The only hybridization of any consequence within the group at the present time is between *Iris versicolor* and *Iris virginica*. Even in this case, there is geographical isolation between the bulk of the two species. Along the eastern seaboard, where the two species have apparently been longest in contact, they are both quite rare. It is only around the Great Lakes, where they are both exceedingly common, that hybridization is at all common. Even here there is partial isolation for the blooming periods of the two species barely overlap. At the northern end of the southern peninsula of Michigan, the two species have evidently been closely associated throughout much of post-glacial time (Anderson '33) and their areas of contact, due to the

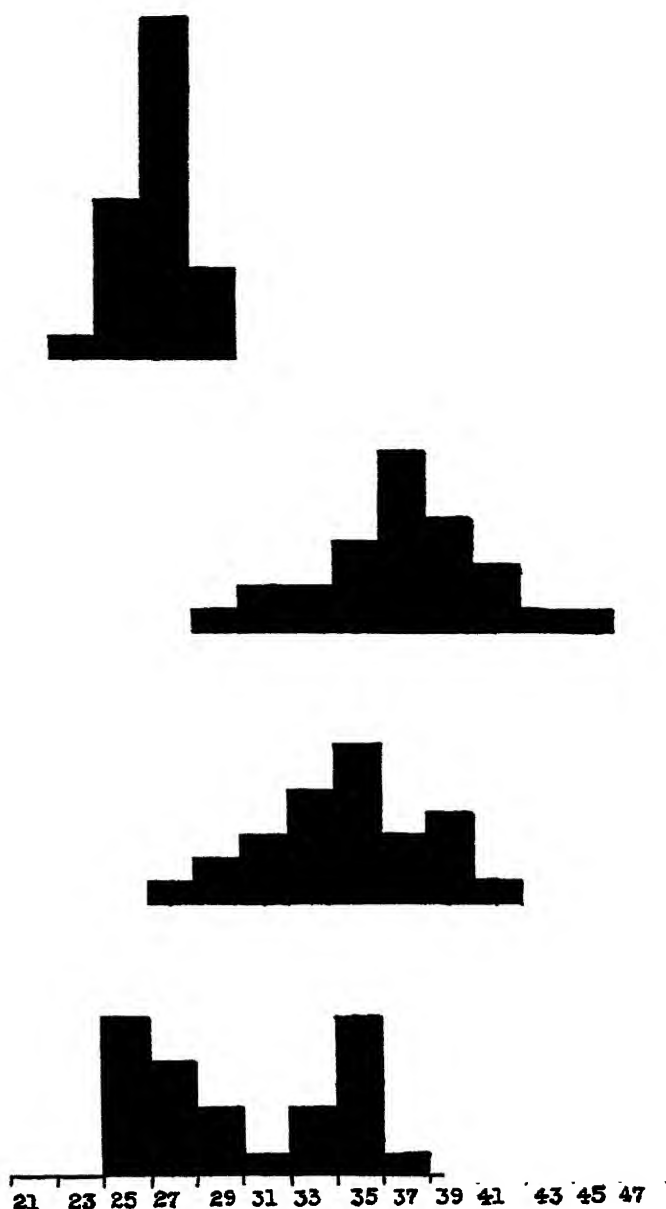


Fig. 14. Frequency distribution for the index, sepal length/petal length + sepal width/petal width, for 27 plants each from the following colonies: Pardeesville, Wisconsin (*Iris virginica* var. *Shrevei*); Billings Bridge, Ottawa, Canada (*I. versicolor*); Engadine, Michigan (hybrids); St. Ignace, Michigan (hybrids).

peculiarities of the various post-glacial lakes, are extremely involved. Even in this area the great majority of colonies are composed exclusively of one species or the other.

On the north shore of Lake Michigan, in an area with a similar post-glacial history, two hybrid colonies were studied in some detail. One was located three miles west of St. Ignace and has since been partially obliterated by relocation of the state road. At this location there were to be found apparently normal *Iris versicolor* and *Iris virginica* and a large number of peculiar intermediates. Few of these resembled the first-generation and second-generation hybrids which had been raised in the experimental plots. Most of them, on the other hand, were very similar to back crosses which had been made between the first-generation hybrids and the two species. This is borne out by fig. 14 where representative colonies of each species are contrasted with these two hybrid colonies, using the following index as a basis for comparison: sepal length/petal length + sepal width/petal width. Figure 14 also shows the very different condition which was encountered at the other hybrid colony which was studied in detail. It was located just west of Engadine, Michigan, and was composed entirely of plants which closely resembled the artificial  $F_1$  hybrids of the breeding plot. Since they also presented the characteristic vigor of such hybrids it is probable that they were for the most part such hybrids, the parental species having been exterminated by their vigorous offspring. It is not impossible, however, that they may represent some new balanced combination of chromosomes. In crosses between such complex amphidiploids as *Iris versicolor* and *Iris virginica* various new polyploid types are not at all unlikely. Unfortunately, the large numbers of chromosomes and the very short period during which the reduction division can be studied (only a few days out of the year) render this rather unprofitable material for such examination.

One can summarize the effect of hybridization between *Iris versicolor* and *Iris virginica* by saying that it does occur very occasionally. Its only effect so far has been a slight blurring of the two species along the zone of contact. It does, however,

provide a means by which new polyploid hybrid species might eventually arise.

Were there fewer technical difficulties involved a detailed analysis of hybridization in these irises would be well worth while, since hybridization is a characteristic part of the phylogenetic pattern throughout the genus. The remarkable phylogenetic tangle of species and hybrids discovered in the Mississippi delta by Dr. J. K. Small is by no means exceptional. Much the same situation exists among the *Pogoniris* species around the Mediterranean; the irises of the *Spuria* group apparently behave in the same way in western Asia; it was perhaps from some such complex that the Japanese irises had their beginnings.

Because hybridization is apparently such an important phylogenetic factor in the genus *Iris*, the hybrids of the Mississippi delta deserve careful analytical study, genetically, taxonomically, and cytologically. It is not enough to prove that hybridization is taking place. Much more important is the determination of its exact role among the Louisiana irises.

The effects of hybridization are various according to the peculiarities of the germ-plasm upon which it is operating and the external conditions under which it takes place. It may result in new amphidiploid species such as *Iris versicolor*. It may produce intermediate swarms which obliterate previous specific boundaries. It may increase the variability of one of the parental species by introducing a small proportion of germ-plasm from the other (Anderson & Woodson, '35, p. 37).

Possibly all of these processes are taking place among the Louisiana irises. It should not be difficult to determine their relative importance and ultimate phylogenetic effects. These irises possess a number of technical advantages for such a study. They have comparatively low chromosome numbers; they are easy to cultivate in experimental gardens; they possess conspicuous specific differences. They are, as Viosca has said ('35), "uniquely adapted for the study of experimental evolution" and one may join with him in predicting a "bright future for them in the study of biology."

To summarize: the evolutionary patterns of the blue flags are fairly typical of the genus as a whole. Seen in a greatly foreshortened view they can be represented graphically as in fig. 13. They form a somewhat tree-like system of cables, the ground pattern occasionally made more complex by amphidiploid cross-connections. The pattern is complicated at one point by inter-specific hybridization. The cables themselves are divided into distinctive cords, the colonies.

Much the same set of patterns would characterize the entire genus *Iris*. The complex knots due to interspecific hybridization would be larger and more significant in certain other portions of the genus; in certain sections the cross-connections of amphidiploidy would be lacking altogether; in a few sections they might be somewhat commoner. All in all, however, fig. 13 may be taken as a fairly accurate representation of phylogenetic relationships for the whole genus. This general similarity of evolutionary patterns within the genus rests upon the fact that the germ-plasm of any species of the genus *Iris* is not a vague generalized germ-plasm. It is *Iris* germ-plasm. It has a number of inherent characteristics which affect speciation and which cause the details of speciation, to be similar throughout (Anderson, '31). It is a genus in which amphidiploidy occasionally occurs, in which every species has a strong development of vegetative propagation, in which inter-specific fertility is the rule. It is, on the other hand, a genus which is ecologically conservative.

Species after species exhibits rather precise demands as to habitat and seems unable to produce variants adapted to more or less moisture, more or less shade, more or less acidity. In the genus *Aquilegia* every species which I have studied extensively is richly provided with ecotypes; sun-forms, shade-forms, types inherently adapted to sour, wet swamps, to sunny, limestone cliffs, to sand dunes, and to woodlands. In *Iris versicolor* and *Iris virginica*, in spite of intensive search, I have been unable to recognize a single ecological variant. Like many genera of the Liliiflorae, the order to which they belong, they are curiously unamenable to ecological differentiation. This conservatism, since it characterizes the whole genus, must rest

upon some inherent property of *Iris* germ-plasm. What that property may be we cannot, as yet, even hazard a guess. It may be that the germ-plasm of *Aquilegia* varies in a way that is unknown or uncommon to the germ-plasm of *Iris*. It may be that due to its ontogenetical organization the genus *Iris*, though possessing the same basic kinds of germinal variation as the genus *Aquilegia*, will nevertheless not respond with variants equipped for other habitats.

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# HYBRIDIZATION IN AMERICAN TRADESCANTIAS

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## FOREWORD

Widely different opinions are held by present-day biologists as to the evolutionary importance of hybridization between species. One of the main reasons for the disagreement seems to be the lack of summarized and codified data bearing upon the problem. This series of papers is not an attempt either to prove or disprove the *importance* of hybridization. It is rather an attempt to gather pertinent data from which to analyze the *effects* of hybridization.

The genus *Tradescantia* has been chosen for two main reasons: (1) Previous taxonomic, cytological, and genetical studies (Anderson and Woodson, '35; Anderson and Sax, '36; Anderson, '36) have indicated the main outlines of the situation in this genus; (2) *Tradescantia* for purely technical reasons is a better object for such investigations than are many other genera of the higher plants, chief among its assets being the facility with which it can be studied cytologically and the ease with which most of the species can be brought into cultivation.

The main object of the investigation, as stated above, has been to procure data from which the importance and the evolutionary rôle of hybridization could be estimated and demonstrated. It had previously been experimentally determined that most of the species allied to *T. virginiana* could be hybridized and that their hybrid progeny were semi-fertile. Similar hybrids had been found in the field and had been subjected to detailed morphological and cytological analysis, but such work was purely preliminary. It merely demonstrated the occurrence of hybridization. What was needed was a method which would determine the dynamics of hybridization in natural populations. In mathematical terms it was necessary to ascertain the frequencies as well as the range of variation (Anderson

and Turrill, '35). That is to say, that we needed to measure and record the effect of hybridization upon the entire population in which it was occurring. Such a method has been evolved and is outlined in section I, while its application to a particular case is demonstrated in section II.

### I. A METHOD FOR MEASURING SPECIES HYBRIDS

Biology employs two methods of measurement, the quantitative and the qualitative. Each has its advantages and disadvantages. Two of the main objections to purely quantitative methods are: (1) quantitative scales are arbitrary and may not bear a direct relation to the phenomenon under investigation, (2) the observational basis of purely quantitative methods is too narrow for many biological problems. It may be well to amplify these *dicta*.

(1) The chief purposes of the quantitative method are to record the variation of certain phenomena and from this record to analyze the forces producing the variation. If a scale has been chosen which is an accurate reflection of the main underlying factors, then the analysis will be a comparatively simple matter. But if the scale used is not in harmony with these underlying causes then it may be difficult, or impossible, to analyze the data. In other words, the data are then no more than a record; a qualitative measure, if objectively defined, would have been quite as efficient. In a paper of fundamental biological significance Wright has demonstrated ('26) how even as simple a transformation as a percentage scale can obscure the interpretation of quantitative data. In many biological problems the customary quantitative scales in which the original observations are recorded are even more inefficient and misleading. The fact that centimeters are equally spaced on the ruler does not mean that variations of a centimeter are always of equal biological magnitude when we use that ruler to measure plants and animals. Purely quantitative measures, lengths, areas, weights, etc., are superior to qualitative units only when they reflect more or less directly the changes in the underlying factors.

(2) As has been pointed out by Minot ('11), the observa-

tional basis of purely quantitative methods is often too narrow for studying biological phenomena. A set of weights, or lengths, is too insignificant an observation to yield sufficient data for exploring a problem. Biology has advanced most rapidly when appropriate qualitative measures have been developed and used with precision. In Genetics, for example, the fundamental data are qualitative. Once obtained they are treated with such precision that most geneticists probably think of their work as purely quantitative. But the fundamental categories, "vestigial" vs. "non-vestigial," "scute" vs. "non-scute," "forked" vs. "non-forked," etc., are quite as qualitative as the fundamental categories of taxonomy. It is because of this fact that they are a broad enough tool to yield useful information about such a complex phenomenon as heredity. If the methods of *Drosophila* genetics were purely quantitative the flies would not be classified in qualitative categories, but their wing lengths, eye diameters, etc., would be laboriously measured. Imagine the difficulties of conducting a *Drosophila* experiment involving two or three wing mutants in which the only available data were the lengths and breadths of the wings! Genetics has been able to advance because it was willing to take the Mendelian recessive (a qualitative unit about whose ultimate significance relatively little was known) and to use that unknown but recognizable entity as a basic unit.

For the study of the species problem a similar combination of qualitative and quantitative methods seems desirable. Few of the differences between species are of the simple sort which are readily amenable to quantitative treatment (Anderson and Whitaker, '34). This is not to say that species do not differ quantitatively. They do, just as do the wing mutants of *Drosophila*, but in both cases it is more efficient to use qualitative categories.

Purely qualitative methods, however, have their own disadvantages. They are often said to be more subjective, but this point is open to argument. Certainly the gene differences by which *Drosophilae* are scored are quite as objective as quantitative measurements. A very real disadvantage in purely qualitative work is that it is not commensurate. One cannot with purely qualitative methods make an accurate com-

parison of the *Iris* plants of one meadow with those of another. What we need for the species problem is a method whose fundamental observations are based upon the qualitative categories of taxonomy but which treats these categories in such a way that they can be used for comparison and analysis. This has been done below in a fairly simple fashion by constructing an index which is the resultant of all the qualitative characters which are readily available.

In the simplest possible case the method operates as follows: Given two species, A and B, the hybridization between which is the object of investigation. Given  $n$  readily ascertainable differences between A and B (as, for instance, position of inflorescence, nature and distribution of pubescence, number of nodes to the stem, distribution of stomata, etc.). For each of these characters an individual plant can be scored as 'a' (like species A); as 'b' (like species B), or as 'i' (intermediate, preferably the actual  $F_1$  if that has been obtained). In particular cases it will be possible to define two or more intermediate grades for the character in question. A hybrid population will be scored somewhat as follows in a case where six distinguishing characters were available:

plant no. 1: a-a-a-i-a-a

plant no. 2: a-a-i-i-b-i

plant no. 3: i-i-i-i-i-i

plant no. 4: b-i-i-i-b-a

and so on for all the plants which are scored. To summarize the population as a whole, all that is necessary is to turn this qualitative scoring into a quantitative index. An index running from complete "A-ness" to complete "B-ness" can be made by arbitrarily giving every 'a' the value of 0, every 'b' the value of 2, and every 'i' the value of 1. This will produce a scale with  $2n + 1$  divisions (in this case 13, i. e., 0 to 12 inclusive. An individual of species 'A' would have an index value of 0 ( $0 + 0 + 0 + 0 + 0 + 0$ ), while an individual of species 'B' would have a value of 12. Plant no. 1 in the above example will have an index value of 1; plant no. 2 a value of 5; plant no. 3 a value of 6; plant no. 4 a value of 7. When the values of each plant

have been computed they can be summarized as a frequency distribution. The frequency distribution constitutes a record of the whole population, in so far as these two species and mixtures between them are concerned. It can be used for the comparison of different hybrid populations and to discover and analyze the forces which are at work in such populations. The index can be varied to fit the available data in various ways. When, for instance, certain of the categories are thought to be more or less reliable than the others they can be appropriately weighted in combining the index. The method seems capable of producing useful and unique data in regard to the variation within and between species. I have used it extensively in the genus *Tradescantia*, one case being published in the second part of this paper. I have also applied it successfully to the analysis of hybridization in *Amelanchier* and *Baptisia* (unpublished). Dr. H. P. Riley has applied it to the hybrid *Iris* populations of the Mississippi delta with interesting results (Riley, in press).

After I had originated the method Dr. Jens Clausen very kindly called my attention to a paper by Raunkiaer ('25) in which an almost identical method of recording the qualitative categories had been applied to a case of hybridization in *Crataegus*. He had not, however, performed the further step of turning the qualitative record into an index, thus making it possible to summarize the population. When this is done the case proves to be a particularly interesting one with certain unique features.

#### SUMMARY

The advantages and disadvantages of quantitative and qualitative methods in biology are discussed. A method of summarizing hybrid populations is developed which utilizes qualitative categories for its initial observations and from these computes a quantitative index value.

#### II. HYBRIDIZATION BETWEEN *T. VIRGINIANA* AND *T. CANALICULATA*

The method developed in SECTION I has already been applied to numerous cases of hybridization in *Tradescantia*. The fol-

lowing one has been selected for preliminary demonstration because it has been analyzed in greater detail and because it is a relatively simple case with no such complicating factors as differences in chromosome number.

*Tradescantia virginiana* L. and *T. canaliculata* Raf. (*T. reflexa* Raf.) are the two commonest Tradescantias of eastern North America. Although each can be cultivated under a variety of conditions they are usually found growing naturally in quite different situations; *T. canaliculata* in the sun, often upon or near rocks or in dry sands; *T. virginiana* in shade or semi-shade. Until white civilization disturbed their natural relationships they seldom or never occupied the same habitat. Even at the present time active hybridization is confined to a very small proportion of either species. The outstanding morphological differences between the two species are as follows (those characters marked with an asterisk \* require the use of a good hand-lens):

<i>T. virginiana</i>	Index value	<i>T. canaliculata</i>	Index value
(1) 2-3 nodes	2	6-8 nodes	0
(2) Sepals broadly ovate, apex broadly acute; calyx inflated after anthesis	2	Sepals elliptic, apex narrowly acute; calyx not inflated after anthesis	0
(3) Sepals and pedicels pubescent throughout	3	Pedicels glabrous; sepals glabrous or barbate	0
(4) * Stomata no more conspicuous than the cells of the upper epidermis	1	* Stomata (and subsidiary cells) much more conspicuous than the cells of the upper epidermis	0
(5) * Stomatal areas of the upper epidermis narrower than the areas without stomata	1	* Stomatal areas much broader than the areas without stomata	0
(6) * Longitudinal distance between stomata longer (often several times as long) than the diameter of a stoma	1	* Longitudinal distance shorter than the diameter of a stoma	0
Total index value	10		0

It was a relatively simple matter to turn these characters into an index, according to the method developed in section I. The figures to the right show in each case the index value assigned to that character. In the case of (3) it was possible to recognize two intermediate grades. If the pedicel was weakly pubescent and the calyx showed the beginnings of a barbate tuft at the apex it was scored as 'vi' (virginiana-intermediate) with an index value of 2; if it had a strongly developed barbate tuft with scattered hairs on the calyx it was scored as 'ci' (canaliculata-intermediate) with an index value of 1. Categories (4), (5), and (6) are given only half the weight of the previous three since they are all different measures of the same quality, the distribution of stomata on the upper epidermis.

It is certainly true of *Tradescantia*, as Wiegand ('35) has observed for *Amelanchier*, that hybridization is much more frequent in areas greatly disturbed by man than under more natural conditions. For that reason an area was chosen for detailed examination in which hybridization between *T. virginiana* and *T. canaliculata* was for the most part taking place under nearly natural conditions. The spot finally chosen is illustrated in Map 1. It is an area two miles square in the township of Joachim, in Jefferson County, Missouri. After the area had been selected it was visited repeatedly by foot and by automobile in an effort to record the exact distribution of all the *Tradescantias* within the four square miles selected. The region is a low plateau, very much dissected by small streams which flow into the near-by Mississippi River. The land has been under cultivation for over a hundred years, the flat hill-tops (plateau remnants) and the rich valley bottoms being for the most part in cultivated crops while the steeper hillsides are left as woodlands or as woodland pasture. The underlying rocks are sedimentary and lie in practically the positions in which they were deposited with little faulting, folding, or tilting. All the strata are limestone with the exception of the St. Peter's Sandstone, here a soft gray-white stone usually exposed as a more or less perpendicular cliff capped with resistant limestone.

The stratigraphy is of considerable importance to the prob-



lem in hand, for it is these steep limestone and sandstone cliffs which constitute the natural habitat for *T. canaliculata*. They are so rocky and dry that not even in the original forest were they fully covered with trees, particularly on southern and western slopes. It will be seen on the map and in fig. 1 that



Map I. Distribution of *T. virginiana* (small closed circles), *T. canaliculata* (large open circles), and hybrids (black and white). The letters A to F indicate places at which detailed collections were made. The line 2-3 represents the position of the section illustrated in fig. 1.

*T. canaliculata* is confined to this narrow belt just below the hill-tops, while *T. virginiana* occurs pretty generally throughout the region on gentle slopes, on hill-tops, and in valley bottoms, but practically always in the shade.

In this particular area *T. virginiana* was much more common than *T. canaliculata*. An effort was made to estimate relative frequencies by computing from the map the areas occupied by

*T. virginiana*, *T. canaliculata*, and the hybrids. These were found to be 16 : 1 : 0.5 respectively.

Thirty plants each of *T. virginiana* and *T. canaliculata* were scored at the localities marked as 'F' and 'B' on the map. The pure species, as can be seen from table I and fig. 2, were relatively invariable and agreed with scorings made at other points in their range. A few hybrid plants were found along the zone of contact between the two species and large hybrid colonies, consisting of fifty or more individuals, occurred at four places, labeled A, C, D, and E on the map. Detailed studies were made at the first two localities.

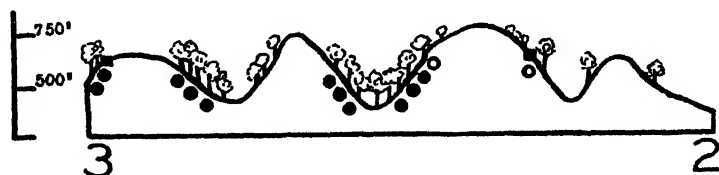


Fig. 1. Diagrammatic section (to scale) along line 2-3 in Map I. Figures to the left show feet above sea-level; closed circles represent *T. virginiana* and open circles *T. canaliculata*. The line is slightly over 2 miles long.

*Locality A.* At this point the public road starts up onto Sandy Ridge along the hard limestone which caps the St. Peter's Sandstone. The latter forms a series of much-weathered cliffs slightly to the south of the road and while the area is pastured, it has not been greatly disturbed of late years. At various points along the cliff a few plants of *T. canaliculata* are growing, and as the road swings to the right the cliffs and the ledge become somewhat shadier by reason of the narrow gorge cut back into the hill by an intermittent stream. At the head of the gorge there is an interesting area of a few hundred square feet in which many kinds of habitats and hence many kinds of plants are brought into close juxtaposition. Rock-plants, prairie grasses, woodland and even desert species are found within a few feet of each other. It is, in other words, exactly the situation in which one might logically expect to find hybridization between ecologically isolated species. Trades-

TABLE I  
SCORING OF INDIVIDUAL PLANTS AT THREE LOCALITIES IN JEFFERSON  
COUNTY, MISSOURI. FURTHER EXPLANATION IN TEXT.

Locality B— <i>T. virginiana</i>															
Plant no.	Categories						Total	Plant no.	Categories						Total
	(1)	(2)	(3)	(4)	(5)	(6)			(1)	(2)	(3)	(4)	(5)	(6)	
1	v	v	v	v	v	v	11	16	v	v	v	v	v	i	10½
2	v	v	v	i	v	v	10	17	v	v	v	v	v	v	11
3	v	v	v	v	v	v	11	18	v	v	v	v	v	v	11
4	v	v	v	i	i	v	9½	19	v	v	v	v	v	v	11
5	v	i	v	v	v	v	10	20	v	v	v	v	v	v	11
6	v	v	v	v	v	v	11	21	v	v	v	v	v	i	10½
7	v	v	v	v	v	v	11	22	v	v	v	v	v	v	11
8	v	v	v	i	v	v	10	23	v	v	v	v	v	v	11
9	v	v	vi	i	v	v	9	24	v	v	v	v	v	v	11
10	v	i	v	v	v	v	10	25	v	v	v	v	i	v	10½
11	v	v	v	v	v	v	11	26	v	v	v	v	v	i	10½
12	v	i	v	v	v	i	9½	27	v	v	v	v	i	v	10½
13	v	v	v	v	i	v	10½	28	v	v	v	i	v	i	9½
14	v	v	v	v	i	v	10½	29	v	v	v	v	v	v	11
15	v	v	v	v	v	v	11	30	v	v	v	v	v	v	11

Locality F— <i>T. canaliculata</i>															
1	c	c	c	c	c	c	0	16	c	c	c	i	i	c	1½
2	c	c	c	c	i	c	½	17	i	c	c	c	c	c	1
3	c	c	c	c	c	c	0	18	c	c	c	c	i	c	1
4	c	c	c	c	i	c	½	19	c	c	c	c	i	c	1½
5	c	c	c	c	c	c	0	20	i	c	c	c	c	c	1
6	i	c	c	c	i	c	1½	21	c	c	c	c	i	c	½
7	c	c	c	c	i	c	1	22	c	c	c	c	c	c	0
8	c	c	c	c	i	i	1½	23	c	c	c	c	c	c	0
9	i	c	c	c	c	c	1	24	i	c	c	c	c	c	1
10	i	c	c	c	c	c	1	25	i	c	c	c	c	i	1½
11	c	c	c	c	c	c	0	26	c	c	c	c	c	c	0
12	c	c	c	c	c	i	½	27	c	c	c	c	c	c	0
13	c	c	c	c	c	c	0	28	c	c	c	c	i	c	1
14	c	c	c	c	i	c	1	29	i	c	c	c	c	c	1
15	c	c	c	i	c	c	1	30	c	c	c	c	i	c	½

Locality A— <i>T. virginiana</i> x <i>T. canaliculata</i>															
1	v	c	ci	c	i	v	3½	16	i	i	vi	i	i	i	6
2	i	c	ci	c	i	c	2½	17	c	c	ci	v	i	i	4
3	i	c	vi	c	i	c	3½	18	i	c	ci	c	i	i	3
4	i	c	ci	c	c	c	2	19	i	i	vi	c	i	i	5
5	i	c	ci	i	i	i	5	20	i	c	ci	i	i	c	3½
6	i	i	vi	c	i	i	5	21	i	i	ci	v	v	c	6
7	i	i	c	c	c	i	2½	22	i	i	vi	v	v	i	9½
8	i	i	ci	v	c	v	6	23	i	c	vi	i	i	c	4½
9	i	c	ci	c	c	i	2½	24	i	i	vi	v	v	i	7½
10	i	c	c	i	i	c	2½	25	i	c	v	i	i	c	5½
11	i	v	ci	c	i	i	5	26	c	c	vi	v	c	i	4½
12	i	v	vi	c	i	i	5	27	i	v	vi	v	v	i	8½
13	i	c	ci	i	i	c	3½	28	i	i	v	c	i	v	6½
14	i	i	c	c	i	i	3	29	i	i	v	v	v	i	7½
15	c	i	c	c	i	c	1½	30	i	c	c	v	c	c	3

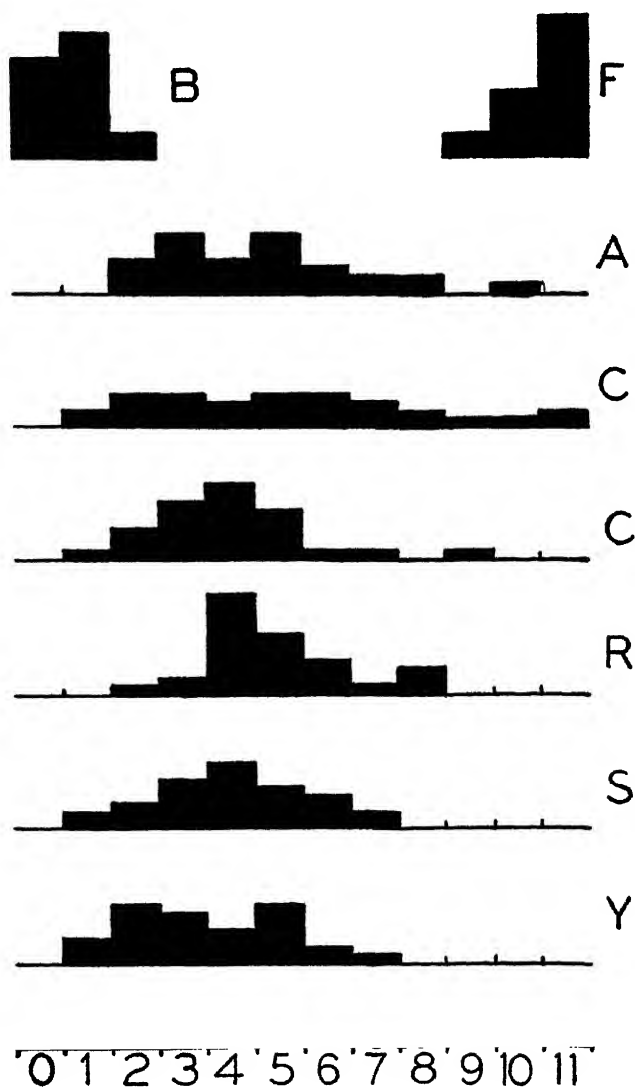


Fig. 2. Frequency distributions for the *virginiana-caniculata* index. Thirty plants each collected at localities A, B, C (two terraces), and F illustrated in Map I; R and S at Algonquin Station, Y at Maplewood, Missouri. Index values shown on the scale at the base of the diagram. B represents a population of pure *T. caniculata*, F a population of pure *T. virginiana*; the remainder hybrid populations. Further explanation in the text.

cantias occur rather generally over the whole area; a few plants of apparently straight *T. virginiana* are growing in the shade of the red cedars and a mongrel population of *T. virginiana*  $\times$  *T. canaliculata* grows in the sunny and semi-shady situations. The cliff at this point is so steep that it was impracticable to collect plants in quantity from the cliff-sides but all of those growing on the ledge were scored in detail. The results are presented in table I and fig. 2, A. (In presenting the frequency distributions only the first thirty plants have been

SCALE	0-1		1			
	2-3	2	1	2	4	4
VALUE	4-5	2	5	2	4	3
	6-7	5	4		2	2
	8-9				2	
		1-2	3-4	5-6	7-8	9-10
		LIGHT INTENSITY				

Fig. 3. Correlation between scale value and the light intensity of the habitat for 46 hybrid plants at locality A. Light intensity in parts of a second required for an equivalent exposure (i. e., scale runs from very shady at left to full sun at the right).

utilized in order to facilitate frequency comparisons with the other distributions.)

The peculiar frequency distribution exhibited by the hybrids at locality A has been found to be generally characteristic of hybrid colonies of *T. canaliculata*  $\times$  *T. virginiana*. It can be conveniently, if somewhat loosely, described by saying that in such populations the hybrids "absorb" the *T. canaliculata* completely but that *T. virginiana* tends to persist in a more or less pure state. It will be seen from fig. 2 that there are no absolutely pure *T. canaliculatae* in spite of the fact that the bulk of the population is much closer to that species than to *T. virginiana*. These must largely be plants which are  $\frac{3}{4}$  or

$\frac{7}{8}$  or  $1\frac{5}{16}$  *T. canaliculata*. At the other end of the scale there is a small proportion of *T. virginiana* but very few or none of the  $\frac{3}{4}$ ,  $\frac{7}{8}$ , and  $1\frac{5}{16}$  *T. virginiana*. As to why the two species should react in this matter one cannot as yet even hazard a guess. Since most of the hybrid populations made up of these two species react in about the same fashion, the reason is probably internal. There seems to be some force or forces which inhibits free recombination between the hybrids and *T. virginiana* and encourages such recombination between the hybrids and *T. canaliculata*. It might possibly be differential pollen-tube growth; it might be a markedly different span of life (both species are perennial); it might be a result of the differences in blooming season (i. e. *T. virginiana* blossoms early and *T. canaliculata* blossoms late. If the hybrids very largely bloomed within the flowering period of the latter species it might produce the observed result).

Among the hybrids those morphologically most like *T. canaliculata* seemed to be growing in the sunniest locations and those most like *T. virginiana* in the shadiest. An attempt was made to measure this objectively and the results are presented in fig. 3 in the form of a correlation table between light intensity and index value. The former was measured with a light meter on a day of uniform cloudiness. The meter was held a foot above the inflorescence and gave readings in fractions of a second required for equivalent exposures. As will be seen from fig. 3, the results indicate that among the hybrids (the pure *T. virginiana* having been excluded) the deeper the shade the greater is the tendency to resemble *T. virginiana*.

At *Locality C* hybridization has produced very similar results. It is a less desirable spot for detailed study since it is adjacent to a state road whose position has been repeatedly shifted and the immediate environment in which the hybrids are found has been subject to violent alterations during the last half century. The cliffs at this point form a series of narrow terraces ten to twenty feet wide and several hundred yards in length. Where the hybrids occur each terrace has evolved a more or less characteristic type. Two collections made on the upper terrace at intervals of fifty feet gave nearly identical

frequency distributions, while nearly adjacent collections from successive terraces showed different distributions. Natural selection is apparently working upon the hybrid population to produce these very local differences. Were this locality less subject to frequent and profound disturbances it would merit a much more detailed analysis.

*Localities D and E* were discovered too late in the flowering season to receive more than a preliminary survey. They apparently present the same general picture as did A and C.

*Tradescantia virginiana* and *T. canaliculata* also hybridize when growing as weeds along railroad rights-of-way, on vacant lots in the city, etc. Several such populations were examined in and near the city of St. Louis in the spring of 1936. Throughout this area *T. canaliculata* is the common weed *Tradescantia*, sometimes occurring along railroad embankments as the predominant plant of early summer for distances of several miles. Occasionally, however, in the immediate neighborhood of open oak woods, *T. virginiana* also contributes to the weed population. Two such hybrid colonies were investigated. Near the Algonquin Station of the Missouri Pacific Railroad two samples (R and S, fig. 2) of thirty plants each were collected between the railroad track and the highway. In Maplewood a sample of thirty (Y, fig. 2) was collected from a vacant lot adjacent to the electric railway. It will be seen that, as in the case of the collections made in Jefferson County, the bulk of the population is composed of individuals which score from 3 to 5 on the scale, individuals in other words which must be about  $\frac{3}{4}$  to  $\frac{5}{8}$  *T. canaliculata*. Hybridization between *T. virginiana* and *T. canaliculata* both along the cliffs and the railroad tracks tends to produce a somewhat variable "*sub-canaliculata*."

#### SUMMARY

Hybridization between *T. canaliculata* and *T. virginiana* was studied at seven localities in Missouri. At these localities there seemed to be a general tendency for the hybrids to "absorb" *T. canaliculata* though *T. virginiana* may persist in a pure state as a small percentage of the population. This is

interpreted as the result of a force or forces, as yet undetermined, which inhibit free recombination between the hybrids and *T. virginiana* and encourage such recombination with *T. canaliculata*.

A general discussion of hybridization is deferred until further cases have been investigated. From data already at hand it is apparent that hybridization, as previously suspected, is very widespread in the genus *Tradescantia*. The details differ somewhat with the conditions of the environment and very greatly according to the species taking part. In certain cases, at least, the resultant variability is so widespread throughout the species, that it must constitute the chief raw material for natural selection. As such it deserves exhaustive observation and critical analysis.

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### THE EFFECT OF ENVIRONMENT UPON THE PRODUCTION OF SPORANGIA AND SPORANGIOLA IN *BLAKESLEA TRISPORA* THAXTER<sup>1</sup>

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The purpose of the following experiments was to study the effects of various environmental conditions upon the production of the two types of sporangia in *Blakeslea trispora*; the large solitary sporangia which possess a columella; and the smaller ones, termed sporangiola, which lack a columella and occur in considerable numbers over the surface of large spherical sporangioliferous heads.

The effect of environment upon the production of sporangia in the Mucorales has already been studied by several botanists. Klebs ('96), working with *Mucor racemosus* which has no sporangiola, studied the effect of quantity and quality of the substrate upon sporangial production, also the effects of humidity, atmospheric pressure, temperature, and light. He discovered that the quantity and quality of the substrate play the dominant rôle in the production of sporangia. Tavel ('86) and Bachmann ('95) reported the effect of nourishment upon the formation of the two types of sporangia in *Thamnidium elegans*. Under favorable conditions of nourishment continued through several generations, the sporangiola became as large and contained as many spores as the sporangia. Conversely,

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with poor nourishment, the terminal sporangia changed into sporangiola, often with but one spore. Brefeld ('91) found that under unfavorable conditions of nourishment the terminal sporangia of *Chaetostylum Fresenii* abort, but that they are again produced under favorable conditions. In *Choanephora*, a genus closely related to *Blakeslea*, little experimental work has been reported, although Cunningham ('79), Couch ('29), Möller ('01), and Thaxter ('14) mention that sporangia are generally produced upon exhausted media.

In *Blakeslea trispora*, first described by Thaxter ('14) and studied in the following experiments, conidia are absent and the sporangia and sporangiola show numerous variations and intergradations. The sporangia vary in diameter from 10 to 80  $\mu$  (pl. 25, figs. 7 and 10). The sporangiola are sometimes borne upon solitary heads at the ends of erect, unbranched sporangiophores, but usually the heads are in groups of 10 or more (pl. 25, figs. 1-5). The sporangiola are typically 3-spored, rarely 4- or 6-spored, and are attached to the heads by a small spherical vesicle. When mature the sporangium falls away, carrying the vesicle with it. The spores are variable in size but in general are alike in all types of sporangia. They are longitudinally striate, and are provided at each end with a cluster of delicate, radiating appendages like those of the sporangiospores of *Choanephora*.

Thaxter ('14) first isolated *Blakeslea trispora* from a culture of *Botrytis* which in turn had been obtained from flowers of the cow-pea. It seems to occur as a weak parasite on various plants (Jochems, '27). It has been shown by Weber and Wolf ('27) to be heterothallic. It is closely related to *Choanephora*. Thaxter homologized the conidia of *Choanephora* with the sporangiola of *Blakeslea*, and suggested that the conidia are to be regarded as monosporous sporangiola. Although he was unable to separate mechanically an outer thin sporangial wall from the conidia of *Choanephora*, his figures of the somewhat abnormal conidia of *C. Cucurbitarum* indicate its existence. In any case, the homology of conidia and sporangia is evident in these genera.

All of the following experiments were performed with two strains of *Blakeslea trispora*. One strain, hereafter called "Strain A," was received through the kindness of Dr. A. F. Blakeslee of the Carnegie Institution of Washington. The other strain, "Strain X," was received from the Centraalbureau voor Schimmelcultures, Baarn, Netherlands. Neither strain deviated greatly from Thaxter's description except that sporangia of the type shown by Thaxter (see pl. 25, fig. 11) were never observed. Both strains produced zygosporoes when crossed with a minus-strain. The strains differed from each other in several respects. Strain X always produced much more mycelium than did Strain A. In Strain X there were always more sporangia than sporangiola, while in Strain A there were always more sporangiola. Strain A produced more yellow-orange pigment upon potato-dextrose agar. There was no discernible difference, however, in the type and size of the spores, sporangia, or sporangiola of the two strains. While the differences do not seem sufficient to warrant a new species, the two strains could always be easily distinguished when grown upon the same petri dish, and their growth reactions often suggested different species.

#### EFFECT OF VARIOUS MEDIA

Both strains were used in all experiments. The various media were made up with distilled water. The petri dish cultures were kept in an incubator which varied daily about one degree from a mean of 23° C. unless otherwise stated. All media and utensils were sterilized at 15 pounds pressure for 30 minutes in the autoclave (to be rid of a species of *Bacillus* which invaded the laboratory during the course of these experiments). Single-spore cultures were started from both strains, using the dilution method outlined by Barnes ('35). Spore suspensions were prepared by transferring 10 loopfuls of sporangiola to 15 cc. of sterile water, and 5 drops of this suspension were used in making inoculations. The estimates of the per cent sporangia or sporangiola are not as exact or as quantitative as our tables indicate. They were made from

counts in three or four sectors of petri-dish cultures, using a binocular dissecting microscope. Two petri dishes were used for each strain. The whole experiment was performed twice, and the results were taken from the two experiments (table I).

The relative numbers of sporangia and sporangiola were the same whether spores from sporangia or sporangiola, or even mycelium, were used as inoculum. In the case of potato-dextrose agar, mycelium five months old, dried, and shriveled, was used, but the culture showed the usual distribution of 65 per cent sporangiola with Strain A. The type of sporangia produced was also unaffected by the number of spores used in inoculation, a colony started with one spore having the same distribution as one with from 50 to 100 spores. Repeated transfers had no effect. A colony started from a dish which was the last of a series of 50 transfers had the same relative number of sporangia and sporangiola as that produced by a direct inoculation of spores from the original culture which had not been transferred. No difference was noted in transfers made by platinum needle or spore suspensions in water, nor did the keeping of spore suspensions in distilled water for three weeks affect the results obtained.

Both strains grew most readily upon potato-dextrose agar and the potato agar. In 48 hours the substrate was covered with mycelia and there was abundant fructification. As is seen from the table, in no case was one type of sporangia produced to the exclusion of the other. Upon all media Strain X produced much more mycelial growth than Strain A. Upon Endo's agar and peptone agar Strain A repeatedly produced a preponderance of sporangiola. Mycelial growth was never dense upon Endo's agar and growth was generally restricted. Although sporangiola as well as sporangia were produced upon this media, the distribution in Strain X was quite different from that in the Strain A.

A potato medium was prepared as follows: 5 cc. potato decoction,<sup>1</sup> 95 cc. distilled water, 2 g. agar, and 2.5 g. sugar. The following sugars were used: dextrose, mannose, galactose,

<sup>1</sup>Prepared by steaming 200 gms. of sliced potato in 1000 cc. of water for one hour. The extract was then decanted, filtered, and made up to one litre.

TABLE I  
EFFECT OF VARIOUS MEDIA UPON TYPE OF SPORANGIA

Medium	Time of appearance of mycelial growth		Time of appearance of fructification		Distribution of sporangia and sporangiola	
	Strain A	Strain X	Strain A	Strain X	Strain A	Strain X
Rat-dung agar	24 hrs.	24 hrs.	No fruiting	No fruiting		
Yeast-dextrose agar	24 hrs.	24 hrs.	No fruiting	No fruiting		
Nutrient agar	24 hrs.	24 hrs.	No fruiting	No fruiting		
Nutritive caseinate agar	24 hrs.	24 hrs.	No fruiting	No fruiting		
Brain-veal agar	24 hrs.	24 hrs.	No fruiting	No fruiting		
Corn-meal agar	24 hrs.	24 hrs.	72 hrs.	72 hrs.	Sporangia 30% Sporangiola 70%	Sporangia 70% Sporangiola 30%
Eosine methylene-blue agar	24 hrs.	24 hrs.	72 hrs.	72 hrs.	Sporangia 30% Sporangiola 70%	Sporangia 70% Sporangiola 30%
Bacto malt-extract agar	24 hrs.	24 hrs.	48 hrs.	72 hrs.	Sporangia 30% Sporangiola 70%	Sporangia 70% Sporangiola 30%
Banana agar	24 hrs.	24 hrs.	72 hrs.	72 hrs.	Sporangia 40% Sporangiola 60%	Sporangia 70% Sporangiola 30%
Endo's agar	24 hrs.	24 hrs.	72 hrs.	48 hrs.	Sporangia 10% Sporangiola 90%	Sporangia 40% Sporangiola 60%
Potato slices	24 hrs.	24 hrs.	No fruiting	No fruiting		
Peptone agar	24 hrs.	24 hrs.	72 hrs.	72 hrs.	Sporangia 10% Sporangiola 90%	Sporangia 60% Sporangiola 40%
Potato agar	24 hrs.	24 hrs.	48 hrs.	48 hrs.	Sporangia 30% Sporangiola 70%	Sporangia 90% Sporangiola 10%
Urea agar	No growth	No growth				
Ammonium-carbonate agar	No growth	No growth				
Starch-dextrose agar	24 hrs.	24 hrs.	72 hrs.	72 hrs.	Sporangia 15% Sporangiola 85%	No growth
Potato-dextrose agar	24 hrs.	24 hrs.	48 hrs.	48 hrs.	Sporangia 35% Sporangiola 65%	Sporangia 85% Sporangiola 15%

maltose, sucrose, lactose, raffinose, rhamnose, arabinose, xylose, and invert sugar. The distribution of sporangial types was not at all affected in Strain A. Upon all the sugars except lactose, raffinose, and mannose, the mycelium was pigmented, while no pigment was produced upon the control (potato agar without sugar). In Strain X there was much more mycelium but no pigmentation. The control with this strain showed all sporangia and no sporangiola. Mannose gave the same results as the control. All the other sugars showed 85 per cent sporangia to 15 per cent sporangiola.

#### EFFECT OF QUANTITY OF FOOD

The two strains reacted differently when grown upon agar with decreasing concentrations of potato. Varying amounts of potato decoction, made as previously, were made up to 100 cc. with distilled water, and 2 per cent agar added. Two petri dishes were used for each food concentration for each strain. A second series was repeated at the critical points. The results are given in table II.

TABLE II  
EFFECT OF QUANTITY OF FOOD UPON TYPE OF SPORANGIA

Potato decoction				
Per cent concentration	Strain A		Strain X	
	Per cent sporangia	Per cent sporangiola	Per cent sporangia	Per cent sporangiola
0.0	50	50	100	0
0.1-1.0	50	50	100	0
1.0-13.0	50	50	100	0
14.0	50	50	90	10
20.	50	50	100	0
40.	40	60	85	15
60.	30	70	70	30
90.	30	70	70	30
Potato-dextrose solution				
0.5	50	50	100	0
1-3	40	60	100	0
5-7	40	60	85	15
10	30	70	85	15
20-100	30	70	70	30

On both media Strain X produced only sporangia with poor food supply. Strain A never produced sporangia alone, although in media with low food supply there were relatively more sporangia and fewer sporangiola. The sporangia produced by both strains with low food concentrations were much smaller than those produced with greater food supply. Most of the sporangia produced upon potato agar between concentrations of 0.5 and 5 per cent were 10–16  $\mu$  in diameter and contained from 10 to 20 spores (pl. 25, fig. 7). Sporangia produced between 10 and 100 per cent concentrations were largely 40–80  $\mu$  in diameter and contained 50–100 spores (pl. 25, fig. 10). Upon the potato-dextrose agar between concentrations of 0.5 and 10 per cent the sporangia were 10–16  $\mu$  in diameter with 10–20 spores. Above 10 per cent they were 40–80  $\mu$  in diameter and contained 50–100 spores.

The concentration of the food also had its effect upon the sporangiola.<sup>1</sup> Between concentrations 0.5 and 5 per cent of potato agar and 0.5 and 2 per cent of potato-dextrose agar there was a predominance of solitary sporangioliferous heads. There were also sporangiola borne upon 2 sporangioliferous heads and a few upon 3 and 4 heads (pl. 25, figs. 1–4). As the amount of food increased, the sporangioliferous heads increased in number until there were as many as 20–30 in the higher concentrations of the two kinds of media (see pl. 25, fig. 5).

As the concentration of food increased the mycelium became more copious, particularly in the case of Strain X. After 70 hours this strain developed a dense mycelium covering the whole petri dish. In the aerial mycelium sporangia 10–16  $\mu$  in diameter began to develop and were very numerous in 4 days. This same type of sporangia appeared with Strain A but de-

<sup>1</sup> Cunningham states concerning the conidial fructifications of *Choanephora Cunninghamiana*: "In cases in which nutrition is imperfect, only a small number of capitella are produced and filaments are encountered with numbers diminished through various degrees until we find specimens with only two capitella. The process of abortion doesn't, however, reach its climax here; for a further stage occurs in which no capitella are produced, and in which the dilated extremity of filament gives direct origin to the sterigmata."



velopment was much slower, from 6 days to 2 weeks being required for a rich growth of aerial sporangia to develop.

Cultures of potato-dextrose agar with good mycelial development were autoclaved, cooled, and reinoculated. After 48 hours, fruiting appeared. In Strain A an equal number of both types of sporangia were produced. Most of the sporangiola were borne upon the solitary sporangioliferous heads (pl. 25, fig. 1). The sporangia were of the small size. Strain X produced no sporangiola and only small sporangia (pl. 25, fig. 7). Mycelium was scant in both strains. Apparently no toxic products of metabolism which inhibit growth were produced, since the results were practically the same as in the small concentrations of nutrient. Warm agar was poured over 6-day-old colonies of Strain A and Strain X grown upon potato-dextrose agar. In 48 hours fruiting appeared in both strains. The results were the same as in the killed cultures. The experiment was repeated with 1, 2 and 5 per cent potato agar with practically the same results. On media with a minimum of food supply, Strain A produced both types of sporangia while Strain X produced one type only.

A final experiment was tried to test the effect of poor nourishment upon the distribution of sporangial types. A piece of mycelium, 1 mm. in length and 3 months old, was transferred to a petri dish containing agar. Other pieces of similar mycelia were transferred to potato-dextrose agar. Fruiting appeared in 48 hours upon the potato dextrose and in 72 hours upon the agar.

TABLE III  
EFFECT OF NOURISHMENT UPON TYPE OF SPORANGIA

Medium	Strain A		Strain X	
	Per cent sporangia	Per cent sporangiola	Per cent sporangia	Per cent sporangiola
Potato dextrose (10 dishes)	35	65	85	15
5 cc. potato broth (10 dishes)	50	50	100	0
Agar (10 dishes)	95	5	100	0

The above table shows the importance of nourishment and its effect upon the type of sporangia produced. Thus in Strain A, it was possible to obtain almost 100 per cent sporangia with very poor nourishment. A single spore culture upon agar-agar produced the same distribution of sporangial types as the piece of mycelium.

#### EFFECT OF HUMIDITY AND OF MOISTURE IN SUBSTRATE

On potato-dextrose agar the fungus produced a predominance of sporangiola about the edge of the petri dishes. This suggested that a dry substrate might help in the production of sporangiola. The dryness was obtained experimentally by varying the amounts of agar.

Strain A was planted on potato-dextrose agar, the concentration of agar in the media being 0.7, 0.9, 1, 1.2, 1.5, 2, 3, 4, 5, 6 per cent. As the concentration increased, the mycelium became heavier and more matted. The distribution of sporangial types was not affected between agar concentrations 0.7 and 3 per cent. The media containing 5 and 6 per cent agar had very much mycelium, but there was a little less than the usual quantity of sporangiola about the edge of the dish. There were numerous sporangia of the smaller dimension (10–16  $\mu$ ) in the aerial mycelium on the petri dishes containing the higher concentrations of agar (5–6 per cent). These experiments were repeated, using two petri dishes for each concentration of agar. The same procedure was followed with Strain X, and here also the growth of mycelium was greater upon the media containing 2 to 6 per cent agar. In the 3, 4, 5, and 6 per cent agar concentrations the mycelium was unusually dense, with a preponderance of sporangia almost entirely in the aerial portion. Only a few sporangiola (4–5 per petri dish) were found in these higher agar concentrations.

The above experiments were repeated with the same series of concentrations of agar in potato decoction. The potato decoction was diluted (1 and 2 cc. solution to 100 cc. distilled water) and made up with the same series of agar concentrations. The results for both strains were the same as in potato-dextrose agar. The distribution of sporangial types remained the same

on the dry media as on the moist—for Strain A about 60 per cent sporangiola to 40 per cent sporangia and for Strain X only sporangia. It was noticed upon the drier substrates that the sporangia and sporangiola were borne upon sporangiophores about 5 mm. longer than the normal ones.

Finally a dilute potato broth (5 cc. potato decoction in 100 cc. distilled water) with the same agar concentrations was used. The distribution of sporangia and sporangiola was not affected, Strain A having 50 per cent of each and Strain X only sporangia. Both strains were then grown upon liquid potato decoction, and fruiting appeared in two days in both. Strain X in 20 tubes produced all sporangia, while Strain A produced 70 per cent sporangiola and 30 per cent sporangia.

The two strains were then grown in different humidities, the procedure of N. Stevens ('16) being followed. Large jars which could be sealed were used as containers. The petri dishes with lids removed were placed in the jars and the jars incubated at 20° C. The media used were potato-dextrose agar and potato agar (5 cc. potato decoction to 100 cc. water). Both strains were grown in the following humidities: 100, 90, 80, 70, 60, 42, 21.5, 10.5 and 2.5 per cent. The distribution of sporangial types was not affected in either strain grown in the range of humidity between 100 and 21.5 per cent. At 10.5 and 2.5 per cent, Strain A showed a slight increase in the number of sporangiola, but this increase was too slight to be of real significance; Strain X was not affected. The strains were also grown in very moist agar in the jar at 100 per cent humidity, without effect upon the distribution; nor was there any difference in distribution when the two strains were grown upon 7 per cent potato agar at 2.5 per cent humidity.

These results in general agree with Bachmann's ('95) prediction that humidity has very little effect upon the production of different sporangial types. However, in growth upon liquid potato broth, sporangia only were produced in Strain X. When this broth was solidified by the addition of agar, the usual distribution occurred, 90 per cent sporangia, 10 per cent sporangiola. Strain A did not behave in this manner.

## EFFECT OF BASIC FUCHSIN

Since growth was rather much restricted for both strains upon Endo's agar, it was thought that the basic fuchsin present in the media might be the cause. In order to see whether such an inhibitor of growth would influence the distribution of sporangial types potato-dextrose agar and potato agar were prepared containing varying amounts of basic fuchsin.

The potato broth was made up by mixing 5 cc. of potato decoction with 100 cc. of water and solidifying with 2 gms. of agar. Basic fuchsin was then added in amounts ranging from .0001 to .01 per cent. At .01 per cent basic fuchsin there was no growth, but as the amount was decreased mycelial growth became more abundant. Fructification did not appear until 72 hours after inoculation. Many of the sporangia and sporangiola did not mature during the whole life of the colony, that is, they remained white throughout their life period. This was especially true when the potato agar contained .005, .004, and .003 per cent basic fuchsin. As far as distribution of sporangial types was concerned, there was only a slight increase in the number of sporangiola in Strain A where the higher concentrations of basic fuchsin were used. With Strain X, the distribution did not seem to be influenced at all, for 100 per cent sporangia was produced, the usual type of fructification when 5 cc. potato solution is used. This experiment was repeated, and two petri dishes were used for each basic fuchsin concentration for both strains. Potato dextrose was next used, the basic fuchsin varying from .0001 to .025 per cent concentration. Strain X did not grow when the dye concentration was .025 per cent, but with the lower concentration the phenomena mentioned above were also observed. There was the same slight increase in sporangiola number for both strains. Mycelial growth was also restricted and the fructifications took much longer to mature, some never maturing. In conclusion, it may be stated that making conditions unfavorable for growth and fruiting by introducing a dye, basic fuchsin, into the substrate does not seem to have any marked effect upon the distribution of sporangial types in either strain.

## EFFECT OF INCUBATION TEMPERATURE

The two strains were inoculated upon potato-dextrose agar and incubated at different temperatures. At 6° C. there was no growth, but at 22° C. normal growth began and the usual types of sporangia resulted in both strains. Low temperature merely suspends activity. The optimum temperature was between 18° C. and 22° C. Between 28° and 36° C., the distribution of sporangial types was not affected but there was a slight increase in mycelium. At 34–36° C. there was very little fructification. When the fungi were incubated at 37° C. only mycelium was produced and at 40° C. there was no growth. The temperature at which strains are incubated seems to have no effect upon the distribution of sporangial types.

## EFFECT OF EXPOSURE OF SPORES TO HIGH TEMPERATURES

The procedure followed in this experiment was similar to that of Barnes ('35) who worked with *Thamnidium elegans*. With a pipette, 0.5 cc. of a spore suspension of both strains was transferred to many tubes. These tubes were exposed to various high temperatures for different time intervals. Two petri dishes were inoculated for each high-temperature exposure for both strains. The whole experiment was performed twice.

The following are temperatures and time intervals at which the strains were exposed:

- 45° C.—1 min., 2 min., 5 min., 10 min., 1 hour, 2 hours.
- 50° C.—1 min., 2 min., 5 min., 10 min., 1 hour, 2 hours.
- 55° C.—1 min., 2 min., 5 min., 10 min.
- 60° C.—1 min., 2 min., 5 min., 10 min., 20 min., 30 min.
- 65° C.—1 min., 2 min., 5 min., 10 min., 15 min., 20 min.
- 70° C.—1 min., 2 min., 5 min., 10 min., 15 min., 30 min.
- 75° C.—1 min., 2 min., 5 min., 10 min., 15 min., 30 min.
- 80° C.—1 min., 2 min.
- 90° C.—15 sec.
- 100° C.—5 sec., 15 sec.

The spores were killed at 80° C. when exposed for one minute. The distribution of sporangial types was not at all affected in either strain by an exposure to high temperature. The only noticeable effect was a retardation in growth and the appear-

ance of fructification at 72 hours instead of the customary 48 hours when the spores were heated at 55° C. and above. Barnes ('35) found that spores of *Thamnidium elegans* yielded variant cultures after exposure to moderately high temperatures, and that the variants preserved their distinguishing characters through a considerable number of transfers. She does not mention whether the high temperature influenced the distribution of sporangia and sporangiola.

Frozen spores were thawed out and inoculated upon potato dextrose and incubated at the optimum temperature. Freezing apparently had no effect upon the distribution of sporangial types.

#### EFFECT OF LIGHT

The two strains were incubated in total darkness and in the light produced by a 60-watt lamp. The distribution of sporangial types was not affected. Light seems to be a stimulus for mycelial growth because those petri dishes in the light always produced much more mycelium than those in the dark.

#### EFFECT OF HYDROGEN-ION CONCENTRATION

Both strains grew best upon slightly acid media. The potato-dextrose agar has a pH of 5.4, and potato agar varied between 5.4 and 5.7. Other media used had various hydrogen-ion concentrations: bacto-malt-extract agar 4.6, potato-dextrose agar 5.4, nutrient caseinate agar 6.5, nutrient agar 6.6, eosine methylene-blue agar and yeast-dextrose agar 7.0, Endo's agar 7.52, bacto brain-veal agar 7.6. The distribution of sporangial types was not affected except on Endo's agar and peptone agar where other factors than hydrogen-ion concentration probably produced the results.

Potato dextrose was then made up with varying amounts of molar potassium hydroxide, and the pH measured by the glass electrode method. The hydrogen-ion concentrations studied were 5.6, 6.2, 7.3, 8.7, 9.6 and 10.2. The distribution of sporangial types was not at all affected by the hydrogen-ion concentration. Neither strain grew upon the media which has a pH of 10.2. At pH 9.6 growth was somewhat restricted, that is, there was less mycelium, but the distribution of sporangia

or sporangiola was not markedly changed. At a pH of 9.6 in Strain X there was a slight increase in sporangiola. Instead of the usual distribution, which is about 70 per cent sporangia and 30 per cent sporangiola, there was about an equal number of both types of fruiting bodies. It should be remembered that Endo's agar has a pH of 7.52, which is slightly on the basic side. Upon that agar there were more sporangiola than upon potato-dextrose agar. The slightly alkaline pH might play a slight role. A medium definitely upon the acid side, as bacto-malt-extract agar with a pH of 4.6, has no effect upon the distribution of sporangial types.

#### SUMMARY

1. Two strains of *Blakeslea trispora* reacted differently to various environmental stimuli. At times, they were so different in growth reactions that it was a temptation to separate the two strains as distinct species.

2. The kind of medium did not seem to have any marked effect upon the distribution of sporangial types, except Endo's agar and peptone agar with Strain A. The formation of sporangiola was favored by these media.

3. The quantity of the food has the most direct influence upon the distribution of sporangial types. With poor nourishment Strain X produced only sporangia. With richer food or with addition of various sugars to potato agar, the sporangiola began to appear. With Strain A it was never possible to obtain one type of reproductive structure to the exclusion of the other—even when agar alone was used. Here the distribution of reproductive structures was half sporangia and half sporangiola. When a tiny piece of mycelium was planted upon agar, there was 95 per cent sporangia to 5 per cent sporangiola. In general, media poor in nutrients favor sporangial formation while those rich in nutrients favor sporangiole formation.

The various other stimuli tried—humidity, moisture content of the substrate, light, hydrogen-ion concentration, freezing and heating of spores, prolonged soaking of spores in distilled water, various methods of inoculation, various incubation temperatures, and frequent transplantation—had no effect upon the distribution of sporangial types. The extent of mycelial

growth and pigmentation were affected by some of these stimuli. In general, the most important factor which determines the type of sporangial fructification is the quantity of food, all other environmental factors mentioned playing a relatively minor role.

This work was done at the suggestion and under the supervision of Professor Carroll W. Dodge in the Henry Shaw School of Botany of Washington University. The writer is greatly indebted to Professor Dodge for many helpful suggestions during the course of the experiments. Also, it is a pleasant duty to acknowledge the help in experimental procedures rendered him by his classmate, Alexander Horwitz.

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## EXPLANATION OF PLATE

## PLATE 25

*Blakeslea trispora* Thaxter.

Figs. 1-4. Sporangioliferous heads produced under conditions of poor nourishment.  $\times 140$ .

Fig. 5. Fructification produced under conditions of abundant nourishment.  $\times 140$ .

Fig. 6. Spore showing cluster of delicate radiating appendages.  $\times 900$ .

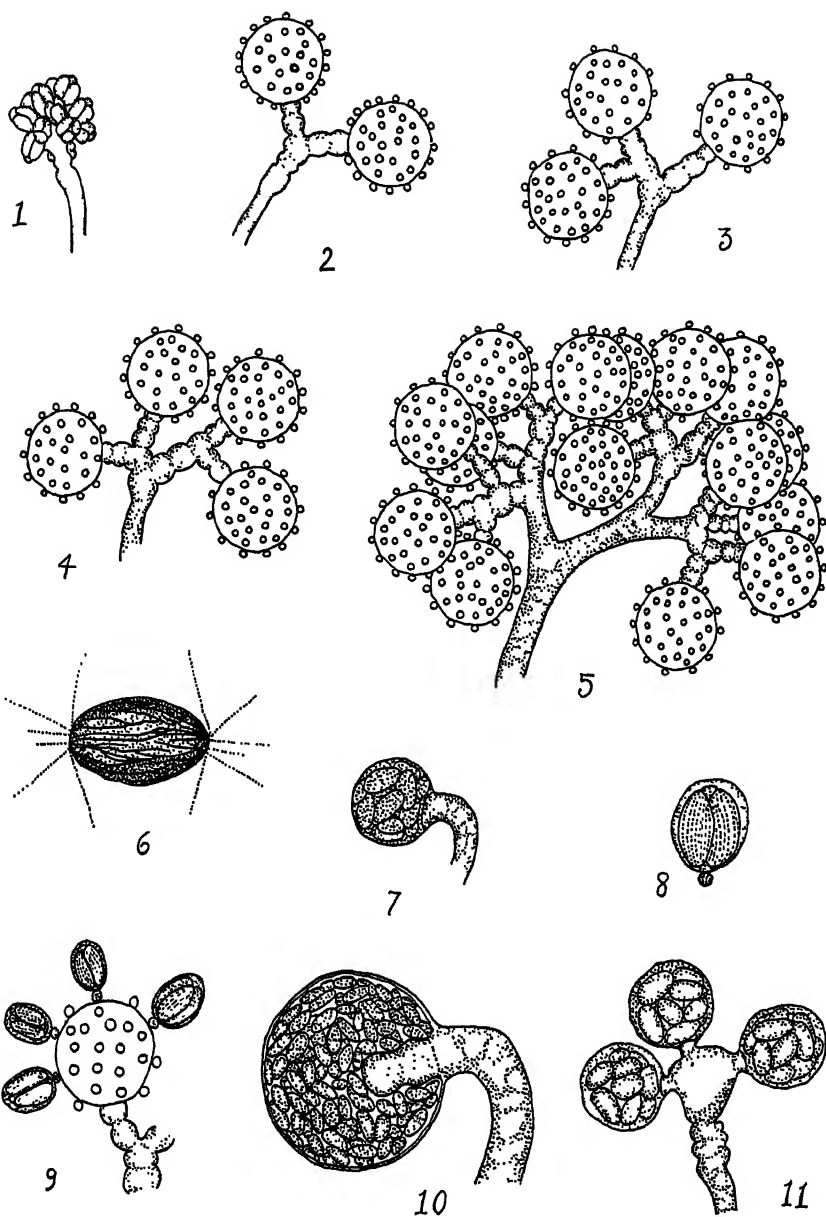
Fig. 7. Smaller type of sporangium with no columella.  $\times 350$ .

Fig. 8. Typical sporangiolum with three spores showing small spherical vesicle which attaches the sporangiolum to the sporangioliferous head.  $\times 490$ .

Fig. 9. Sporangioliferous head with adhering sporangiola.  $\times 250$ .

Fig. 10. Larger type of sporangium with columella.  $\times 250$ .

Fig. 11. Type of sporangium figured by Thaxter but never observed by the writer, which greatly resembles the sporangiolar type of fructification.  $\times 240$ .





# NEW ORGANISMS OF CHROMOMYCOSIS<sup>1</sup>

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The organisms of the disease chromomycosis (chromoblastomycosis of Terra, Torres, da Fonseca & Arêa de Leão), or dermatitis verrucosa, have received little comparative study. Except for the recent investigations of Carrión and Emmons, no attempts have been made to point out definite morphological relationships among these microbes. The only well-established fungus of the group is *Phialophora verrucosa* Thaxter, which has been isolated only twice in the United States and once in Uruguay. Another organism treated in several publications, *Acrotheca Pedrosoi*, is the only agent of chromomycosis of South America, according to a number of mycologists. A Brazilian pathogen from this disease, studied by French workers, was first named *Hormodendron Pedrosoi* Brumpt, and later the name was changed to *Trichosporium Pedrosianum* by Ota, and then to *T. Pedrosoi* by Langeron. This microbe, considered to be identical with other Brazilian fungi causing chromomycosis, has led to some taxonomic confusion.

While in São Paulo, Brasil, the opportunity was presented to make a comparative study of a number of cultures of fungi isolated from cases of chromomycosis in South America and in North America, in the laboratory of the junior author. As a result of an intensive examination of these pathogens, the fol-

<sup>1</sup> Work made possible through a fellowship granted by the John Simon Guggenheim Memorial Foundation to the senior author, for study in South America, 1935-1936.

lowing conclusions were arrived at: First, *Phialophora*, as described by Thaxter, not only exists in South America, as was pointed out by MacKinnon in Uruguay, but an original strain studied by Pedroso and Gomes (named *P. verrucosa* by these workers and then changed to *Acrotheca Pedrosoi* by other South American investigators) was found to be a new species, *Phialophora macrospora*. Second, *Hormodendron Pedrosoi* Brumpt (*Trichosporium Pedrosoi* Langeron) shows sufficient characters other than those of the genus *Hormodendron* to form a new genus, *Hormodendroides*, with *H. Pedrosoi* as the type species. Third, *Gomphinarina Pedrosoi* (Brumpt) Dodge (*Acrotheca Pedrosoi* of Terra, Torres, da Fonseca & Leão), an organism which was considered identical with *Hormodendron Pedrosoi*, was found to have characteristics simulating those of the genus *Botrytis* and also certain features not belonging to that genus. For these reasons the genus *Botrytoides* is described as new, but since *Pedrosoi* is the specific name for the type species of *Hormodendroides* the name *monophora* is given to the type species of the new genus. Fourth, an organism isolated in Brasil from a case of chromomycosis has the characteristics of all the above genera: the "cup" formation common to *Phialophora*, the conidiophores common to *Botrytoides*, *Hormodendroides*, and *Hormodendron*, in addition to the superimposition of the "cup" formation on the *Hormodendron* conidiophores. This fungus is here described as a new genus, *Phialoconidiophora*. It is given the specific name of *P. Guggenheimia* in honor of the Foundation which made the work possible. The organism *Hormodendron compactum* Carrión is no doubt of this same genus, but differs sufficiently in cultural features and mycelial measurements to be a new species, *Phialoconidiophora compactum* (Carrión) Moore & Almeida, n. comb.

Although not entirely in favor of establishing a number of new genera for a group of organisms which show close relationships in certain aspects, yet the authors feel that the so-called "lumping" or grouping of several distinctly different microbes in the same genus adds only to the existing confusion in the taxonomy. Hence the following new genera are de-

scribed provisionally until a mycological classification is established which will allow for a taxonomic differentiation of such organisms.

The fungi are here described with English and Latin diagnoses. A more complete and illustrated discussion will follow in a later publication.

***Phialophora macrospora* Moore & Almeida, sp. nov.**

*Phialophora verrucosa* A. Pedroso & J. M. Gomes, Bull. Soc. Med. Cir. São Paulo 3: 254. 1920; Gomes, *ibid.* 3: 42, 43. 1920; Ann. Paulistas Med. Cir. 11: 53–61. 1920.

*Acrotheca Pedrosoi* Terra, Torres, da Fonseca & Arêa de Leão, Brasil Medico 2: 363–368. 1922.

This species differs from *P. verrucosa* in the size of the spores and “cups.” Spores large, spherical, ovoid or ellipsoid, elongate or short, variable in form and size; spherical up to 7  $\mu$  in diameter, ellipsoid 2–4  $\times$  3–7  $\mu$ . Hyphae branched, septate, 2–6  $\mu$  in diameter. Spore-bearing cups 2–7  $\mu$  in diameter at lips, chiefly 4–5  $\mu$ . Oidoid cells approximately 5  $\mu$  in diameter. Spherical cells on Loeffler’s agar 6–14  $\mu$  in diameter, usually 12  $\mu$ . Color of colonies grayish-brown, olivaceous-green to black.

Differt ab *P. verrucosa* in magnitudine sporarum phialarumque. Sporae magnae, multiformes, sphaericae, ovoideae vel ellipsoideae, elongatae vel breves; sphaericae ad 7  $\mu$  diametro; ellipsoideae 2–4  $\times$  3–7  $\mu$ . Hyphae ramosae, septatae, 2–6  $\mu$  diametro. Phialae 2–7  $\mu$  diametro ad labias, plerumque 4–5  $\mu$ . Oidia circiter 5  $\mu$  diametro. Cellulae sphaericae in “Loeffler’s agar” 6–14  $\mu$  diametro, plerumque 12  $\mu$ . Color “grayish-brown,” “olivaceous green” vel nigrum.

***Botrytoides* Moore & Almeida, gen. nov.**

Simulates *Botrytis* morphologically but differs in the blue-black color of culture. Hyphae repent, branched, septate, submerged on most substrates. Conidiophores simple or branched or proliferating, brown with simple, irregular tips due to presence of small continuations of conidia (sterigmata of some authors) which remain after conidia mature and separate from conidiophore. Conidia fusiform to short-cylindric,

several attached close together at the tip of the conidiophore, brown or subhyaline in color.

Hoc genus *Botrytidi* similis, differt in culturis atris. Hyphae repentes, ramosae, septatae, plerumque submersae. Conidiophorae simplices vel ramosae proliferantesve, fulvae, simplicibus irregularibusque cum apicibus, sterigmatibus minutis persistentibus tectis. Conidia fusiformia aut brevia, cylindrica, catervatim plerumque apicalia, fulva vel subhyalina.

The genus *Campsotrichum*, generally considered to be a dematiaceous *Botrytis*, is to be differentiated from *Botrytoides* on the basis of conidiophore morphology and spore distribution. The conidiophores of *Campsotrichum* terminate in short, bifurcated branches with the spores arranged on short branchlets, as contrasted with the simple or branched conidiophores of *Botrytoides*.

The type species of this genus is:

***Botrytoides monophora* Moore & Almeida, sp. nov.**

*Phialophora verrucosa* A. Pedroso & J. M. Gomes, Bull. Soc. Med. Cir. São Paulo 3: 254. 1920; Gomes, *ibid.* 3-42, 43. 1920; Ann. Paulistas Med. Cir. 11: 53-61. 1920.

*Hormodendron Pedrosoi* Brumpt, Précis Parasitol. ed. 3. 1921.

*Acrotheca Pedrosoi* Terra, Torres, da Fonseca & Arêa de Leão, Brasil Medico 2: 363-368. 1922.

*Trichosporium Pedrosianum* Ota, Jap. Jour. Derm. Urol. 28<sup>+</sup>: 6. 1928. (In Emmons, 381-423, Abs. in Fr. 16-23.)

*Trichosporium Pedrosoi* Langeron, Ann. Parasitol. Hum. Comp. 7: 145-150. 1929.

*Gomphinarina Pedrosoi* Dodge, Med. Myc. p. 850. 1935.

Colonies dark, greenish-gray, olivaceous-green to black with a brown or purple tinge. Conidiophores single or multicelled, lateral or terminal. Spores ovoid, ellipsoid, or subfusiform,  $1\frac{1}{2}$ -5  $\times$  2-8  $\mu$ , arranged along the conidiophore or in head formation. Hyphae of regular, irregular, or sclerotic cells, 2-5  $\mu$  in diameter, depending on medium grown.

Culturae obscurae, viridi-cinereae, "olivaceous-green" vel nigrae, fulvescentes purpurascencesve. Conidiophorae uni-aut multi-cellulae, laterales aut terminales. Sporae ovoideae, ellipsoideae aut subfusiformes,  $1\frac{1}{2}$ –5  $\times$  2–8  $\mu$  diametro, in conidiophoris aut in capitibus dispositae. Cellulae hypharum regulares aut irregulares aut scleroticae, 2–5  $\mu$  in mediis diversis.

**Hormodendroides** Moore & Almeida, gen. nov.

Mycelium black, septate, branched. Conidiophores of two types: simple with conidia fusiform to short-cylindric, several attached on irregular, thickened, terminal portion of conidiophore; and conidiophores of *Hormodendron* type with spores catenulate in acrogenous branches, subspherical or ellipsoid.

Mycelium nigrum, septatum, ramosum. Conidiophorae biformes: (1) simplices, conidiis pyriformibus vel breve-cylindricis, aliquot in irregulare crassata terminale parte conidiophorae junctis; (2) ramosae *Hormodendro* similes, sporis catenulatis, acrogenis, subsphericis aut ellipsoideis.

The type species is *Hormodendron Pedrosoi* Brumpt.

**Hormodendroides Pedrosoi (Brumpt)** Moore & Almeida, comb. nov.

*Hormodendron Pedrosoi* Brumpt, Précis Parasitol. ed. 3. 1921.

*Acrotheca Pedrosoi* Terra, Torres, da Fonseca & Arêa de Leão, Brasil Medico 2: 363–368. 1922.

*Trichosporium Pedrosianum* Ota, Jap. Jour. Derm. Urol. 28<sup>4</sup>: 6. 1928.

*Trichosporium Pedrosoi* Langeron, Ann. Parasitol. Hum. Comp. 7: 145–150. 1929.

*Gomphinarina Pedrosoi* Dodge, Med. Myc. p. 850. 1935.

**Phialoconidiophora** Moore & Almeida, gen. nov.

This genus differs from *Phialophora* by the presence on various media of the three types of conidiophores: dendroid, branching conidiophores of the *Hormodendron* type, with "cupulliform" spore-bearers generally produced at the apices of the "conidiophores," but sometimes laterally; and conidiophores of the *Botrytoidea* type; and also by the "cupulli-



form" spore bearers of the *Phialophora* type. Cells (chlamydospores) of the type seen in tissue. Spores from "cups" globoid to ovoid, small, hyaline to subhyaline and held together by a mucilaginous substance; spores from conidiophores of *Botrytoides* type ovoid, ellipsoid, or subfusiform, larger than the above; spores of *Hormodendron* type catenulate in acrogenous branches, subspherical or ovoid. Hyphae branched and septate.

In mediis diversis hoc genus differt ab *Phialophora* in conidiophoris dendroideis ramosis, *Hormodendro* similibus, et phialis plerumque apicalibus vel aliquot lateralibus; et conidiophoris *Botrytoidi* similibus; et sporophoris phialidis *Phialophorae* similibus. Cellulae (chlamydosporae) eis in hospite similes. Sporae ab phialis globoideae vel ovoideae, parvae, hyalinae vel subhyalinae, materia mucilaginosa cohaesae; sporae conidiophoris *Botrytoidi* similibus ovoideae, ellipsoideae vel subfusiformes, maiores quam eae in *Botrytoidi*; sporae *Hormodendro* similes catenulae in ramis acrogenis, subsphaericae vel ovoideae. Hyphae ramosae et septatae.

The type species of the genus is:

***Phialoconidiophora Guggenheimia* Moore & Almeida, sp. nov.**

Mycelium aerial or submerged. Cultures olivaceous-green, grayish-black tinged with purple or black. Hyphae  $2-4\frac{1}{2}$   $\mu$  in diameter, bearing conidia  $1\frac{1}{2}-4\frac{1}{2} \times 3-8$   $\mu$ , sessile, single and isolated, or on short to long, single or multicelled, warty conidiophores, simple, branched, or proliferating, of *Botrytoides* type. Conidiophores of *Hormodendron* type with smooth to warty "foot cells" of various proportions, bearing several phialides approximately  $2-4 \times 4-10$   $\mu$ , with conidia  $1\frac{1}{2}-4\frac{1}{2} \times 3-8$   $\mu$ , Phialae  $2-6$   $\mu$  in diameter at lips, borne either on specialized branches or developing directly from hyphae or on stalks, one to several-celled; spores mostly hyaline, globoid  $1-3$   $\mu$  in diameter, ovoid  $1-2\frac{1}{2} \times 2-4$   $\mu$ . Oidioid cells  $4-7$   $\mu$  in diameter or long axis. Bundles of hyphae (coremioid) with hyphae  $2-3\frac{1}{2}$   $\mu$  in diameter. Sclerotic cells of various proportions. Chlamydospores thick-walled, single or multilocular, approximately  $3-16 \times 3-16$   $\mu$ , some larger on various media.

Mycelium aerium aut submersum. Culturae "olivaceous green," "grayish black" purpurascentes vel nigrescentes. Hyphae  $2-4\frac{1}{2}$   $\mu$  diametro. Conidia  $1\frac{1}{2}-4\frac{1}{2} \times 3-8$   $\mu$ , sessilia, singula aut in conidiophoris multicellulis verrucosis simplicibus ramosis aut proliferantibus *Botrytoidi* similibus. Conidiophorae *Hormodendro* similes cellulis basalibus laevibus vel verrucosis, diversae magnitudine, phialides circiter  $2-4 \times 4-10$   $\mu$  ferentae, cum conidiis  $1\frac{1}{2}-4\frac{1}{2} \times 3-8$   $\mu$ . Phialae  $2-6$   $\mu$  diametro ad labias, sessiles, in conidiophoris aut in stipibus, uni aut pluri-cellulae. Sporae subhyalinae vel plerumque hyalinae, globoideae,  $1-3$   $\mu$  diametro, ovoideae  $1-2\frac{1}{2} \times 2-4$   $\mu$ . Oidia  $4-7$   $\mu$  diametro in axe longo. Hyphae in fasciculis  $2-3\frac{1}{2}$   $\mu$  diametro. Cellulae scleroticae diversae magnitudine. Chlamydo-sporae cum muris crassis, singulae, multiloculatae,  $3-16 \times 3-16$   $\mu$ , aliquando maiora in mediis diversis.

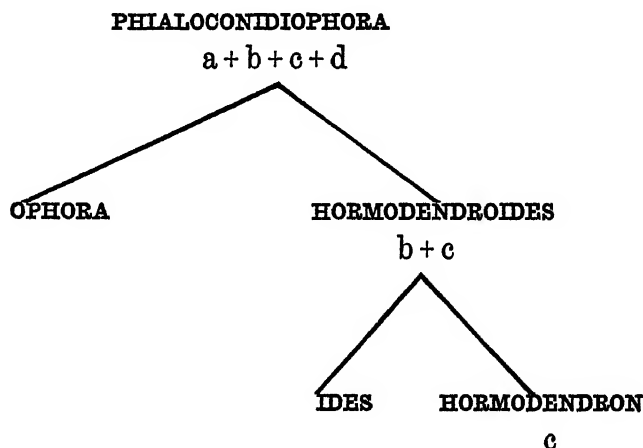
***Phialoconidiophora compactum*** (Carrión) Moore & Almeida, comb. nov.

*Hormodendrum compactum* Carrión. A. L. Carrión, Puerto Rico Jour. Publ. Health 10: 543-545. 1935; *ibid* 11: 663-681 (679-681). 1936.

Hyphae long, coarse,  $2.5-5.2$   $\mu$ , arborescent, with occasional dichotomous branching. *Hormodendron* sporulation predominant; *Phialophora* type rare. Conidia in former spherical or subspherical, smooth, olivaceous, borne in short branching chains, in compact groups at tip of conidiophores,  $2.5-4.8 \times 2.5-3.8$   $\mu$ . Basal elements in chains  $3.8-6 \times 3-4.5$   $\mu$ . Conidiophore of *Phialophora* type  $7-12 \times 3-4$   $\mu$ . Conidia  $1.5-2 \times 2-3$   $\mu$ , oval, smooth, thin-walled and light green in color. Growth on Sabouraud's agar slow, colonies 2.5 cm. in diameter after 6 weeks. Abundance of aerial hyphae, amber in color. Colonies on 4 per cent dextrose agar similar except for a smoother, more velvety appearance. Colony on Czapek's agar poorly developed, with a diameter of 10-16 mm. at end of 6 weeks. Mycelium in substrate olive-black.

The generic relationship in question here can be brought out more clearly if the phylogeny is considered speculatively. Assuming that the organism with the most complicated life cycle

is the oldest, and the simplest the youngest, then we can trace a direct descent of one group from another. If we let "a" represent the "cup" formation of *Phialophora*; "b" the conidiophores of *Botrytoides*; "c" the conidiophore of *Hormodendron*; and, "d" the compound formation of the "cup" formation of *Phialophora* superimposed, as it were, on the conidiophore of *Hormodendron*, then the schematic arrangement is greatly simplified as follows:



NOTE. Since this paper went to press the authors have found that Bonorden spelled the genus name *Hormodendrum* and not *Hormodendron* as they and most medical mycologists have given it. The spelling should be changed throughout this paper.



## EXPLANATION OF PLATE

## PLATE 26

- Fig. 1. "Conidiophore" of *Phialophora macrospora* with emerging spore.  
Fig. 2. "Conidiophores" of *P. macrospora* with groups of spores  
Fig. 3. Conidiophores of *Botrytoides monophora*  
Fig. 4. "Conidiophores" of *Phialoconidiophora Guggenheimia*, of *Hormodendron* type with cups of *Phialophora* type  
Fig. 5. Enlarged "conidiophore" showing "cupuliform" spore bearer  
Fig. 6. Mycelium of *P. Guggenheimia* showing: a. conidiophores of *Botrytoides* type. b. "cupuliform" spore bearer. c. *Hormodendron* type of spore formation. d. conidiophore of c.



MOORE & ALMEIDA —NEW ORGANISMS OF CHROMOMYCOSIS



## NEW GENERA OF CLADOCHYTRIACEAE

GEORGE ZEBROWSKI

The thallophytes described in this paper are believed to be fungi belonging to the family Cladochytriaceae. They all possess a definite hyphal mycelium and either terminal, subterminal, or intercalary enlargements which frequently contain spores and assumedly are sporangia. The thalli proliferate within the limy matrix of Echinoderm spicules, shells of molluscs, and foraminifera, and within the spicules of calcareous sponges. The entire fungus is buried within the substrate and communicates with the exterior only by means of single pores which open into the sporangial sacs. All the described forms were found by the writer about two years ago in calcareous Australian sand associated with such fossils as *Globigerina*, *Textularia*, *Nodosaria*, *Lagena*, and *Spiroloculina*. Their age, therefore, may range from Cambrian to recent. The samples of sand were obtained from Ward's Natural Science Establishment, Rochester, N. Y., and were collected at Ninety Mile Beach in South Victoria, Australia.<sup>1</sup>

<sup>1</sup> It is to be regretted that neither the collector of these fungi, nor their exact location could be determined. The labels accompanying the samples of sand merely stated "Ninety Mile Beach, South Victoria, Australia." The party collecting these sands has died, and no additional information was available. To clear up their origin, the writer dispatched an inquiry to Sir Douglas Mawson, at the University of Adelaide, which elicited the following reply:

"The locality 'Ninety Mile Beach, South Victoria,' is not specifically correct for either of the two Ninety Mile Beaches figuring on our maps. There is such a beach at Gippsland, Victoria, where it faces the Pacific Ocean. But there is another Ninety Mile Beach in South Australia which faces the Southern Ocean, and extends east from the mouth of the Murray River.

"I can't imagine how Wards got a sample from the South Australian Ninety Mile Beach and think it most likely that yours came from Gippsland. I will therefore get in touch with F. Chapman, Palaeontologist of the National Museum, Melbourne, who is an authority on foraminifera and much interested in marine sands. He may be able to get some Gippsland beach sand for you.

"As for our Ninety Mile Beach sand I will take the first opportunity to enlist the services of any scientists going that way—and hope to procure some for you. It is an out-of-the-way place, however, there being no settlement near that long line of coast."



The type and cotype specimens have been deposited in the herbarium of the Missouri Botanical Garden, St. Louis.

The writer acknowledges his indebtedness for aid and suggestions in carrying out this study to Dr. Charles Lyman Porter, of Purdue University, and Dr. Carroll William Dodge, of the Henry Shaw School of Botany of Washington University. The photomicrographs accompanying this article are partly the work of Dr. Edwin Jacob Kohl.

**DODGELLA** Zebrowski, gen. nov.

Hyphae intramatricales in ostracis, ex base spherica ramosae, perpendicularibus hyphis sporangiferis; dehiscencia ignota; sporangiosporae sphaericae.

Type: *Dodgella priscus* Zebrowski.

Hyphae rarely branched, growing beneath the surface of shells and in sponge spicules, proliferating from the spherical base of the sporangia which are subterminal with the longitudinal axis at right angles to the hyphae, dehiscence unknown; sporangial neck reaching surface of the shell or spicule and opening by a pore to the outside; sporangiospores ? spherical.

This genus is closest to *Nowakowskiella* and *Cladochytrium*, but the branching is different, also the attachment of the sporangium to the hypha. This genus is named in honor of Dr. Carroll W. Dodge.

**Dodgella priscus** Zebrowski, sp. nov. Pl. 27, figs. 1, 3.

Thallus sphericus, levis, 2-9 hyphas gignens; sporangia 15  $\mu$  diametro, cervix ad 5  $\mu$  longitudine, apertura apicale ad 3.5  $\mu$  diametro; sporangiosporae? rarae, sphaericae, brunneae?, ad 3  $\mu$  diametro.

Thallus a simple, smooth, globular sac, about 15  $\mu$  in diameter, from which emerge 2-9 distributive hyphae; sporangial necks short, about 5  $\mu$  long, communicating with the surface by a circular aperture about 3.5  $\mu$  in diameter; sacs usually empty, occasionally showing red or brown, spherical spores? averaging 3  $\mu$  in diameter.

This interesting fungus is of wide and seemingly cosmopolitan distribution. The writer found it in sands of both fossil

and recent formations from such widely separated localities as South China Sea, South Australia, Texas (Eocene formation), Africa, and from beach sands around Beaufort, North Carolina. The specimens from the different localities vary somewhat in size, but the variations are so slight that it has not been possible to resolve them into more than a single species. This species has been found growing on the shells of molluscs and ostracoda and within the spicules of sponges (pl. 27, fig. 3).

This fungus shows a tendency toward rapid proliferation and the formation of extensive colonies, being the most abundant species. The mature sac sends off one or more reproductive hyphae from its globular base. These grow for varying distances just below the surface of the substrate and eventually each hypha produces a new sac, subterminal in position and from 5 to 15  $\mu$  back from its tip. This daughter sac then grows down into the substrate at right angles to the hypha and in turn it produces new hyphae from its globular base. Occasionally sacs are also produced at the tips of hyphae. The hyphae are about 1  $\mu$  thick, of uniform diameter, and branch but rarely.

When spores were dissolved on a slide with dilute hydrochloric acid, those from a single sac remained cemented together in a clump, some degree of force being required to separate them with a dissecting needle. Further, spores similar to those within the sacs were found scattered over the surfaces of a number of pieces of shell. Most of these spore-like bodies not only adhered to the surface, but were embedded in spherical cavities of varying depths. It seems likely that the spores secrete some substance which enables them to adhere to the shells on which they may lodge and develop. Occasionally a hypha would end in a bifurcation consisting of two comma-shaped swellings, thickest at their free ends. It is possible that these are gametangia.

**Dodgella inconstans** Zebrowski, sp. nov. Pl. 27, fig. 2.

Hyphae 1  $\mu$  diametro, subramosae; sporangia 15–22  $\times$  27–44  $\mu$ , irregularia, subterminalia, ampulliformia, lobata, subapplanata, cervicibus perpendicularibus, ostiolis circularibus, 4  $\mu$  diametro.

Hyphae occasionally branched,  $1\ \mu$  in diameter, sterile hyphae rare; young sporangia subterminal, flask-shaped, growing straight down into the substrate, the bottom soon becoming lobed or folded and usually somewhat flattened, so that the neck is at right angles to the venter,  $15-22 \times 27-44\ \mu$ ; ostioles single, circular, averaging  $4\ \mu$  in diameter; no spores seen. One large colony, however, showed the sporangia more or less completely filled with an amorphous, brown substance with black spots, resembling protoplasm.

On shells of molluscs in tidal beach sands, Beaufort, North Carolina, of recent origin.

The sporangia are extremely variable in size and shape in this species.

**Dodgella radicans** Zebrowski, sp. nov. Pl. 27, fig. 4.

Hyphae  $1\ \mu$  diametro; sporangia  $17-21 \times 27-43\ \mu$ , subterminalia, pyriformia, ostiolis circularibus,  $4\ \mu$  diametro, rhizoideis 4-15, plerumque 8, longitudine variabilibus, irregulariter sparsis; sporae non visae.

Hyphae of uniform diameter, about  $1\ \mu$ , usually 2 or 3 distributive hyphae and 4 to 15, usually 8 rhizoids to each sporangium; sporangia  $17-21 \times 27-43\ \mu$ , subterminal, pyriform, opening to the surface of the shell by a single circular ostiole about  $4\ \mu$  in diameter; spores not seen.

In shells of molluscs in fossiliferous sands from Ninety Mile Beach, probably Victoria, Australia.

**COULTERELLA** Zebrowski, gen. nov.

Hyphae intramatricales praelongae, tenuissimae, in ostracis molluscorum; sporangia fusiformia vel bifurcata (literae Y similia); sporae pachydermaticae, sphaericae vel subsphaericae.

Type: *Coulterella Petersoni* Zebrowski.

Intramatrixal hyphae very long, slender, in shells of molluscs; sporangia fusiform or forked (in a single plane similar to the letter Y); spores thick-walled, spherical or flattened, abundant.

This genus differs from the preceding in the shape of its spo-

rangia which are often forked and communicate with the surface by a common pore. The genus is named for Dr. Stanley Coulter.

**Coulterella Petersoni** Zebrowski, sp. nov. Pl. 27, fig. 12.

Hyphae 270–730  $\mu$  longitudine, aequales, ad 1  $\mu$  diametro; sporangia 68–98  $\times$  20–27  $\mu$ , simplicia fusiformiaque vel bifurcata (literae Y similia), poro singulo commune aperta, ad 5  $\mu$  diametro; sporangiosporae copiosae, subapplanatae, junioribus leptodermaticis, ad 5  $\mu$  diametro, maturis pachydermaticis, ad 4  $\mu$  diametro, rubro-brunneis.

Hyphae long, 270–730  $\mu$ , uniform in diameter, about 1  $\mu$ ; sporangia 68–98  $\times$  20–27  $\mu$ , either simple and fusiform or proliferating in a single plane to form Y-shaped structures opening to the surface by a common pore about 5  $\mu$  in diameter; sporangiospores abundant both in the primary sporangium and its branches, somewhat flattened, thin-walled, slightly greenish in appearance, 5  $\mu$  when young, becoming thick-walled, reddish, averaging about 4  $\mu$  in diameter when mature.

Found in shells of molluscs. This species is named in honor of Prof. Perry S. Peterson.

*Coulterella Petersoni* is a common form resembling *Conchyliastrum Enderi* in its development. The thallus is a flattened sac, with only 1–3 similarly flattened diverticula which usually give rise to two or more distributive hyphae. The diverticula or lateral sacs are more irregular in outline in this species than they are in *Conchyliastrum Enderi*; also, two or more hyphae may emerge from each diverticulum, which was never observed in *Conchyliastrum*, where the hyphae arise singly as distal prolongations of the lateral sacs. In both genera the daughter sacs are formed one to each hypha, usually sub-terminal in position. Each daughter sac then develops into a primary sac. Each primary sac in turn gives rise to one or more lateral pouches which lie in the same plane and appear to be only prolongations of the main sac; in *Conchyliastrum Enderi* the pouches are usually at an angle or at right angles to the main sac. When only one pouch develops, the resulting thallus is fusiform, but with two

pouches, the thallus is roughly Y-shaped (pl. 27, fig. 12). The daughter thalli remain attached to the parent by means of the distributive hyphae which occasionally branch. The numerous spores of this species were found closely packed both in the primary sacs and in the diverticula. Two kinds of spores were observed, a thick-walled, red spore averaging  $4\ \mu$  in diameter, and a larger, thin-walled, greenish spore  $5\ \mu$  in diameter. This last was assumed to be immature. Both types are somewhat flattened.

**PARAMOECIELLA** Zebrowski, gen. nov.

Hyphae longae, ramosae, ramis perpendicularibus; sporangia elongata intercalaria, somati Paramoecii similia, levia, leptodermatica; sporae non visae.

Type: *Paramoeciella Gamblei* Zebrowski.

Hyphae branched, alternate, rarely opposite, perpendicular to the axis of the main hypha, bearing large, intercalary, elongate sporangia, shaped like the body of *Paramoecium*, but smooth and thin-walled; spores not seen.

These large intercalary sporangia, shaped like the body of *Paramoecium*, seem quite distinct from any genus so far reported.

**Paramoeciella Gamblei** Zebrowski, sp. nov. Pl. 27, figs. 5-6.

Hyphae  $7\ \mu$  diametro, longae, infrequenter ramosae, intramaticales; sporangia intercalaria, elongata,  $193\text{--}214 \times 280\text{--}962\ \mu$ , somati Paramoecii similia, sed levia, leptodermatica; sporae non visae.

Hyphae long,  $7\ \mu$  in diameter, infrequently branched, usually alternate, rarely opposite, branches at right angles to the main axis, thickened at the base; sporangia intercalary, elongate, closely resembling *Paramoecium* in outline,  $280\text{--}962 \times 193\text{--}214\ \mu$ , each sporangium arising as an elongate swelling on one side of a hypha, with its long axis parallel to that of the main hypha and attached at its side for about one fourth its length; hyphae occasionally seen arising directly from the sporangium (pl. 27, fig. 6); large oval aperture averaging  $34\ \mu$  in width and tapering toward the sac developing at the point of contact; en-

tire thallus smooth and thin-walled, without spines or other irregularities; no spores observed.

This species was quite common and usually occurred in clusters of sporangia and hyphae as shown in pl. 27, fig. 5. It is named for Dr. Dean La Fever Gamble.

**ARTHURELLA** Zebrowski, gen. nov.

Hyphae intramatrales; sporangia elongata, tubularia, terminalia, longis cum cervicibus, poris apicalibus, proliferantia; sporangia partialia, spherica vel pyriformia, irregulariter distributa; sporae in sporangiis lateralibus (partialibus), sphaericae.

Type: *Arthurella Corringtoni* Zebrowski.

Hyphae intramatrix; sporangia elongate, tubular, terminal with long tapering necks, opening by an apical pore, proliferating to form spherical or pyriform, partial sporangia irregularly distributed over the primary ones; spores spherical, seen only in the lateral (partial) sporangia.

The genus is named in honor of Dr. Joseph Charles Arthur.

**Arthurella Corringtoni** Zebrowski, sp. nov. Pl. 27, fig. 10.

Hyphae 3–4  $\mu$  diametro; sporangia elongata, tubularia, 48–119  $\times$  13–24  $\mu$ , terminalia, longis cum cervicibus, poris apicalibus 5  $\mu$  diametro, proliferantia; sporangia partialia spherica vel pyriformia, irregulariter distributa, magnitudine variabilia; sporangia magna una cum partialibus echinulata; sporae in sporangiis lateralibus (partialibus) aureae, sphaericae, 3  $\mu$  diametro.

Hyphae 3–4  $\mu$  in diameter, tapering only slightly, usually thickened at point of emergence, occasionally branched, arising only from main sporangium; sporangia 48–119  $\times$  13–24  $\mu$ , with long tapering necks and apical pores 5  $\mu$  in diameter, proliferating to form partial sporangia which are pyriform or spherical, irregularly distributed along the main sporangium, variable in size, perhaps produced progressively as the sporangium elongates; larger sporangia and portions of adjacent hyphae covered with very small spines, observable only under high magnifications in larger specimens and assumedly char-

acteristic of maturity; lateral (partial) sporangia always much smaller than main sporangium, varying from 6 to 14; spores found only in the partial sporangia, golden in color, spherical, averaging  $3\ \mu$  in diameter.

This species is named for Dr. Julian Dana Corrington.

**CONCHYLIASTRUM** Zebrowski, gen. nov.

Hyphae ex apicibus sporangiorum secundariorum, longae, nova sporangia gignentes; sporangia secundaria fusiformia, elongata, radiata ex ventro globoso sporangii primarii cum ostiolo singulo cervice longa; sporae ovoideae, pachydermaticae.

Type: *Conchyliastrum Enderi* Zebrowski.

Primary sporangia subterminal, flask-shaped, with a long neck and round venter which proliferates to form long-fusiform, secondary sporangia with ovoid, thick-walled sporangio-spores; hyphae arising from tips of secondary sporangia, spreading through the shell, and giving rise subterminally to another group of sporangia.

The genus name is derived from the Latin *concha* (shell) and *aster* (star).

**Conchyliastrum Enderi** Zebrowski, sp. nov. Pl. 27, figs. 7, 9.

Hyphae longae, 255–527  $\mu$ , ad 1  $\mu$  diametro; sporangia primaria 20  $\mu$  diametro, spherica, cervicibus cum tubularibus, 30  $\mu$  longitudine, et poris apicalibus circularibus, 5  $\mu$  diametro, proliferantia; sporangia lateralia, partialia, 2–14, plerumque 6–7, radiata, 34  $\times$  7  $\mu$ , elongata, fusiformia vel ampulliformia; sporae 3  $\mu$  diametro, ovoideae, rubro-luteae, pachydermaticae.

Hyphae long, 255–527  $\mu$ , 1  $\mu$  in diameter; primary sporangia 20  $\mu$  in diameter, spherical, with tubular necks 30  $\mu$  long, and apical, circular pores 5  $\mu$  in diameter, proliferating; lateral or partial sporangia, 2–14, usually 6–7, radiating, 34  $\times$  7  $\mu$ , elongate, fusiform or flask-shaped; spores 3  $\mu$  in diameter, ovoid, reddish-yellow, thick-walled.

Found in the calcareous parts of molluscan shells and in sponge spicules. This species is named for Dr. Howard E. Enders.

If the matrix is thick and permits of uncrowded development, the thallus develops a long-necked, flask-shaped, primary sac from the globular base of which radiate the lateral pouches (pl. 27, fig. 7). If, however, the matrix is too thin to permit of deep growth and normal expansion, the thallus will spread out in a single plane like the fingers of a hand (fig. 9). From the distal extremities of the lateral sacs emerge single hyphae which penetrate the matrix for long distances, eventually giving rise to new subterminal sacs (fig. 7). These daughter sacs elongate, become flask-shaped, develop lateral pouches and hyphae, and thus give rise to a new thallus.

**Conchyliastrum Merritti** Zebrowski, sp. nov. Pl. 27, fig. 11.

Hyphae crassae, 5–3  $\mu$  diametro, ax apicibus sporangiorum partialium proliferantes, breves; sporangia primaria clavata, intercalaria, 75  $\times$  30  $\mu$ , cervicibus longis, poris apicalibus 5  $\mu$  diametro, irregulariter proliferantia; sporangia lateralia (partialia) 50  $\times$  10  $\mu$ , fusiformia, dein irregulariter subspherica; sporae brunneae, 1  $\mu$  diametro, sphaericae, catervatae in sporangiis primariis secundariisque.

Hyphae thick, 5  $\mu$  in diameter, tapering to 3  $\mu$ , proliferating from the tips of the partial sporangia, short; primary sporangia clavate, intercalary, 75  $\times$  30  $\mu$ , with long necks and apical pores 5  $\mu$  in diameter, irregularly proliferating to form secondary sporangia 50  $\times$  10  $\mu$ , fusiform at first, becoming irregularly subspherical; spores brown, 1  $\mu$  in diameter, spherical, collected into spore balls, seen both in the primary and in the secondary sporangia.

In its general structure and development this species resembles *C. Enderi*, but there is a lack of symmetry in the lateral pouches. They seem to arise as spindle-shaped outgrowths but soon become irregularly globular, no two being alike in shape and some as large as the primary sporangium. The hyphae are relatively short and stout, emerging as prolongations of the lateral sporangia so that it is difficult to tell where they begin. They also taper in their course, being about 5  $\mu$  thick at their origins and about 3  $\mu$  at their distal ends.

This species is named for Mr. Edgar B. Merritt.



**ARBORELLA** Zebrowski, gen. nov.

Hyphae dichotome ramosae, rhizoideis; sporangia terminalia, spherica, poris magnis; sporae non visae.

Type: *Arborella Kohli* Zebrowski.

Hyphae dichotomously branched, bearing minute rhizoids at the nodes; sporangia terminal, large, spherical, with a large pore; spores not seen.

The generic name was given because of a fancied resemblance of this form to a branch of a tree with fruit at its extremities.

**Arborella Kohli** Zebrowski, sp. nov. Pl. 27, fig. 8.

Hyphae dichotome ramosae, 1.6  $\mu$  diametro, 20–70  $\mu$  inter ramis, rhizoideis ad 1  $\mu$  diametro; sporangia spherica, 10  $\mu$  diametro, poris magnis; sporae non visae.

Hyphae dichotomously branched, 1.6  $\mu$  in diameter, 20–170  $\mu$  between nodes, rhizoids about 1  $\mu$  in diameter; sporangia spherical, 10  $\mu$  in diameter, with large pores; spores not seen.

The main hyphae and branches are all about the same thickness and of somewhat irregular outline. The internodes vary in length and are thinner than the nodes. Each internode bears one or more rhizoidal hairs which penetrate the substrate and apparently emerge on the opposite side of the shell. The entire thallus lies buried within the living matrix of the shell. The sporangia are spherical with large pores of approximately the same diameter as that of the sac, which open on the same surface as the rhizoidal hairs.

This species is named for Dr. Edwin Jacob Kohl.

**Arborella Calverti** Zebrowski, sp. nov.

Hyphae dichotome ramosae, 1.4  $\mu$  diametro, ad 132  $\mu$  inter ramis, rhizoideis longis; sporangia elongata, irregulariter lobata, 12–33  $\mu$  diametro, sine poris; sporae non visae.

Hyphae dichotomously branched, 1.4  $\mu$  in diameter, about 132  $\mu$  between nodes, with long coiled rhizoids; sporangia elongate, irregularly lobed, 12–33  $\mu$  in diameter, apparently rupturing irregularly, without a well-defined pore; spores not seen.

The main hyphae bearing the sporangia lie beneath one sur-

face of the shell. The rhizoids arise from both nodes and internode and penetrate within the matrix, producing an abundant, tangled network of threads. Frequently a node gives rise to both a sporangiferous branch and a rhizoid.

The species is named for Dr. Phillip Powell Calvert.

## EXPLANATION OF PLATE

## PLATE 27

Figs. 1 and 3 *Dodgella priscus*

Fig. 2. *Dodgella inconstans*

Fig. 4. *Dodgella radicans*

Figs 5 6 *Psamocrella Gambler*

Figs 7 and 9 *Conchylastrum Enderi*.

Fig. 8 *Arborella Kohl*

Fig 10 *Arthurella Corringtoni*

Fig 11 *Conchylastrum Merritt*.

Fig. 12 *Coultella Petersoni*.



ZEBROWSKI—NEW GENERA OF CLADOCHYTRIACEAE



# HYDNANGIUM AND RELATED GENERA<sup>1</sup>

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In continuation of our studies on the Hymenogasteraceae (*sensu latiore*) we present here and in the following paper<sup>2</sup> the genera belonging to the Hydnangiaceae as defined by Dodge,<sup>3</sup> except *Lycogalopsis* of which we have seen too little authentic material to present at this time. Malençon<sup>4</sup> proposed the family name Asterogasteraceae for essentially this same group, although he notes that *Sclerogaster* is very aberrant, and apparently he overlooked *Maccagnia* and *Lycogalopsis*. He would also include the gymnocarpous Russulaceae in the same series Astérosporés. *Hydnangium* has had a relatively simple tradition since its first description, although from time to time discordant elements have been referred to it. The small generic segregates are easily recognized. Since all the genera have not been included here, due to lack of authentic material, we prefer to postpone a discussion of generic relationships until more data are available. The key on the next page will serve to identify material in this and the following paper:

<sup>1</sup> Published as Technical Paper No. 254, with the approval of the Director of the Oregon Agricultural Experiment Station. Contribution from the Department of Botany in cooperation with the Henry Shaw School of Botany of Washington University.

<sup>2</sup> Zeller, S. M., and C. W. Dodge. *Elasmomycetes, Arcangeliella, and Macowanites*. *Ann. Mo. Bot. Gard.* 23: 599-638. 1936.

<sup>3</sup> Gäumann, E. A., and C. W. Dodge. Comparative morphology of fungi. 701 pp. McGraw Hill Book Co., New York, 1928. (See pp. 485-488.)

<sup>4</sup> Malençon, G. La série des Astérosporés. *Trav. Cryptog. dédiés à Louis Mangin*, 377-396. *pl.* 39. 1931. (See p. 392.)

Issued January 8, 1937.

1. Fructification angiocarpous, but peridium is sometimes absent from a narrow space about the stipe in *Arcangeliiella*..... 2
1. Fructification hemiangiocarpous, the lower portion of the gleba completely exposed at maturity.....*Macowanites* (p. 636)
2. Sterile base present and highly developed at maturity, lignicolous; tropical.....*Lycogalopsis*
2. Sterile base sometimes present when young but not highly developed and persistent; terrestrial (except *Sclerogaster luteocarneus*)..... 3
3. Spores very thick-walled, appearing smooth under lower magnifications, but minutely echinulate to verrucose under higher powers..... 4
3. Spores thinner-walled, alveolate to echinulate or rugose..... 5
4. Latex absent, columella usually absent.....*Sclerogaster* (p. 566)
4. Latex present, columella present.....*Maccagnia* (p. 573)
5. Columella absent, spores echinulate to echinate..... 6
5. Columella present, spores alveolate to echinate..... 7
6. Spores spherical or nearly so, echinulate to echinate....*Hydnangium* (p. 574)
6. Spores long-ellipsoid, echinate with a broad collar at the base.....  
.....*Stephanospora* (p. 597)
7. Latex absent, spores echinulate.....*Elasmomyces* (p. 600)
7. Latex present, spores alveolate, rugose, or echinulate....*Arcangeliiella* (p. 602)

We have used the same color standards, and cited the specimens with the same abbreviations as in our previous work.<sup>5</sup> Besides those whose aid was gratefully acknowledged in previous papers, we are indebted to Mrs. Olive Rodway for the loan of material from the Rodway Herbarium at the Tasmanian Museum. For financial assistance we are grateful to the American Association for the Advancement of Science (grant in 1923 to the junior author), and to the John Simon Guggenheim Memorial Foundation, which appointed the senior author a fellow to Europe in the autumn of 1930, and to the Science Research Fund of Washington University (grant to the senior author in 1933).

#### SCLEROGASTER

*Sclerogaster* Hesse, Hypog. Deutschl. 1: 84-86. 1891; Sacc. Syll. Fung. 11: 170. 1895; Bataille, Bull. Soc. Myc. France 39: 180. 1923; Coker & Couch, Gasteromycetes Eastern U. S. & Canada, 25-26. 1928; E. Fischer, in Engler & Prantl, Die Nat. Pflanzenfam. ed. 2, 7a: 18. 1933.

The type species of the genus is *Sclerogaster lanatus* Hesse.

<sup>5</sup> Dodge, C. W., and S. M. Zeller. Hymenogaster and related genera. Ann. Mo. Bot. Gard. 21: 625-708. pl. 18. 1934. (See pp. 625-627.)

Fructifications small, white, embedded in a thick, flocculent mycelium, attached by rooting fibrils; peridium usually soft; gleba usually pale yellowish, gelified, drying very hard, cavities small, usually filled with spores similar to *Leucogaster* in shape; basidia small, cylindric to clavate, sterigmata short; spores small, thick-walled, spherical, appearing smooth under lower magnifications but mostly minutely echinate to verrucose under higher powers.

This well-marked genus seems to form a transition between *Leucogaster* and *Hydnangium* or *Arcangeliiella*. The spores are much smaller than the average in the above genera and have a relatively thicker wall. In some species there are faint suggestions of a columella but no lactiferous ducts have been seen. In general appearance the fructifications resemble *Leucogaster* but have very minute cavities. They have usually been included in *Hydnangium* (*Octaviania* Auct. non Vitt.) on account of the echinate spores.

The species seem confined to Europe, with one species in southeastern United States, one in tropical America, and one in Oregon and California. Each species seems quite limited in its distribution.

#### KEY TO SPECIES OF SCLEROGASTER

1. Peridium separable..... 2
1. Peridium not separable..... 4
  2. Peridium duplex, layers separating readily at maturity; spores 4-6  $\mu$  in diameter.....1. *S. lanatus* (p. 568)
  2. Peridium of thin-walled pseudoparenchyma.....2. *S. pacificus* (p. 568)
  2. Peridium of loosely tangled hyphae in a gel..... 3
3. Peridium 180-250  $\mu$  thick.....3. *S. hysterangioides* (p. 569)
3. Peridium about 300  $\mu$  thick.....4. *S. Broomeianus* (p. 569)
  4. Peridium not more than 100 $\mu$  thick..... 5
  4. Peridium 100-200  $\mu$  thick..... 6
  4. Peridium more than 350  $\mu$  thick.....5. *S. luteocarneus* (p. 570)
5. Spores 6-8  $\mu$  in diameter; peridium of loosely tangled hyphae.....
  - .....6. *S. candidus* (p. 570)
5. Spores 4-5  $\mu$  in diameter; peridium of loose periclinal hyphae.....
  - .....7. *S. siculus* (p. 571)
  6. Spores 7-9  $\mu$  in diameter, verrucose; peridium 140  $\mu$  thick, of periclinal hyphae.....8. *S. minor* (p. 572)
  6. Spores 6-7  $\mu$  in diameter, smooth or nearly so; peridium 180  $\mu$  thick, of periclinal hyphae.....9. *S. liospermus* (p. 572)



6. Spores  $4-6\ \mu$  in diameter, finely echinate; peridium  $120-140\ \mu$  thick, of loosely tangled hyphae.....10. *S. compactus* (p. 573)

1. *SCLEROGASTER LANATUS* Hesse, Hypog. Deutschl. 1: 85-86. 1891, excl. syn.

Illustrations: Hesse, Hypog. Deutschl. 1: *pl. 5, f. 11*.

Type: in Herb. Bot. Inst. Univ. Marburg, a fragment in Dodge Herb.

Fructifications up to 1 cm. in diameter, spherical, snow-white, woolly; peridium duplex, inner layer of the same texture as the trama, about  $280\ \mu$  thick, the outer layer  $40\ \mu$  thick, of more loosely woven hyphae with abundant crystal deposits tearing away in places; gleba snow-white at first, becoming apricot-yellow, hard; cavities small, not filled with spores; septa about  $35\ \mu$  thick, of slender periclinal hyphae embedded in a gel; basidia cylindric,  $14 \times 4\ \mu$ , 4-8-spored; sterigmata short; spores spherical,  $4-6\ \mu$  in diameter, thick-walled, smooth or nearly so.

Under duff in coniferous woods. England and Germany. May to October.

The type seems still rather immature; at least cavities are still being formed at the inner portion of the "peridium."

GERMANY: Hessen-Nassau, Cassel, *E. Hesse*, 1887, type (Hesse and Dodge).

ENGLAND: Kent, Orford, *C. E. Broome* (Broome Herb. at Kew).

2. *SCLEROGASTER PACIFICUS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

Type: in Zeller and Dodge Herbaria.

Fructifications subspherical, drying 0.8-1.0 cm. in diameter, dirty white; sterile base present; columella not seen; peridium evanescent, about  $100\ \mu$  thick, pseudoparenchymatous, cells up to  $200 \times 30\ \mu$ , very thin-walled; gleba firm, finally friable, ochraceous-buff; cavities polyhedral, filled with spores; septa of loosely woven, slender hyphae in a gel, thin,  $20-30\ \mu$  thick; basidia clavate, soon collapsing and evanescent; spores spherical, with very large verrucae, 9-10 per great circle,  $7-8\ \mu$  in diameter.

This species seems aberrant in some respects, with its sterile base and gleba finally becoming friable, but it seems more closely related here than elsewhere.

OREGON: Coos County, Bandon, S. M. Zeller 7425, type (Zeller and Dodge).

3. *SCLEROGASTER HYSTERANGIOIDES* (Tulasne) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

*Hydnangium hysterangioides* Tulasne, Fung. Hypog. 76. 1851; DeToni in Sacc. Syll. Fung. 7: 177. 1888.

*Octaviania hysterangioides* Lloyd, Myc. Notes 67. 1141. 1922.

Illustrations: Tulasne, Fung. Hypog. pl. 21, f. 5.

Type: in Broome Herb. at British Museum, a slice from type in Lloyd Museum, material from the same locality and collector at the same date, agreeing wholly with the description but determined as *Octaviania compacta* Tul., in the J. W. Bailey Collection at Brown University.

Fructifications small,  $0.6 \times 0.4$  mm. when dry, dirty white, surface flocculent, drying slightly rugose; peridium 180–250  $\mu$  thick, composed of loosely tangled hyphae embedded in a gel; gleba maize-yellow to buff-yellow or light brownish-olive in young material; cavities minute,  $100 \times 300$   $\mu$ , filled with spores in the older specimens; septa hyaline, easily scissile, 7–10  $\mu$  thick between hymenia, composed of slender, gelified hyphae; basidia clavate,  $12 \times 6$   $\mu$ ; sterigmata short; spores small, spherical, slightly echinulate, appearing smooth under the lower powers of the microscope, hyaline to dilute cream-color in mass, 4.5–6.5  $\mu$  in diameter.

ITALY: Rome, C. E. Broome (under *Octaviania compacta* Tul., Brown Univ. 56, and Farlow); Rome, Panfilo Gardens, C. E. Broome, 1846, type (Brit. Mus., Kew, and slide from type in Lloyd Mus.).

4. *SCLEROGASTER BROOMEIANUS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

*Octaviania compacta* Massee, Ann. Bot. 4: 32–33. 1889 [often cited as Monogr. Brit. Gast.].

Illustrations: Massee, Ann. Bot. 4: pl. 1, f. 12.

Type: in Broome Herb. at British Museum and Berkeley Herb. at Kew.

Fructifications  $0.5 \times 0.3$  cm., depressed-globose, white; peridium separable, 280  $\mu$  or more thick, composed of a prosenchyma of hyphae 3–4  $\mu$  in diameter; gleba isabella-color or

dark olive-buff, with minute cavities filled with spores; septa scissile, 20–30  $\mu$  between hymenia, of slender, loosely woven periclinal hyphae embedded in a gel; basidia clavate, 7–8  $\times$  3–4  $\mu$ , with short sterigmata; spores spherical, thick-walled, minutely and sparsely echinate, 5–7  $\mu$  in diameter.

Among grass roots. Southern England. October and November.

EXSICCATI: Rabenhorst, Fung. Eur. 2502.

ENGLAND: Gloucestershire, Leigh Wood, C. E. Broome, type (Brit. Mus. and Kew); Kent, Shoreham, C. E. Broome, distributed in Rabenhorst, Fung. Eur. 2502.

5. *SCLEROGASTER LUTEOCARNEUS* (Bresadola) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

*Octaviania luteocarpa* Bresadola, Ann. Myc. 18: 54. 1920; Trotter in Sacc. Syll. Fung. 23: 601. 1925.

*Arcangeliella luteocarpa* Lloyd, Myc. Notes 67: 1142. 1922; Rick, Egatea 19: 111. 1934.

Type: in Lloyd Museum.

Fructifications subspherical or obovate, 0.7–1.0 cm. in diameter, smooth, yellowish flesh-color becoming brownish; sterile base conical, about 3 mm. tall, forming the suggestion of a columella; peridium not separable, loose, stipose, 360–380  $\mu$  thick, with outer mycelial patches composed of periclinal hyphae next the gleba and on the outside, with tangled thick-walled hyphae between; gleba yellowish flesh-color; cavities polyhedral; septa white, composed of hyphae 3–4.5  $\mu$  in diameter; basidia clavate, 22–24  $\times$  6–7  $\mu$ ; spores spherical, tuberculate-echinulate, 6–7.5  $\mu$  in diameter, often with the remains of the sterigma 2–3  $\mu$  long.

On wood. Tropical America.

GUADELOUPE: Bois de Bains Jaunes, Duss, 1895 (Berlin and Farlow).

BRAZIL: Rio Grande do Sul, Poco das Antas, J. Rick 51, type (Lloyd Mus. 60625, and Dodge).

6. *SCLEROGASTER CANDIDUS* (Tulasne) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

*Hydnangium candidum* Tulasne, Ann. Sci. Nat. Bot. II. 19: 376. 1843; Fung. Hypog. 75. 1851; DeToni in Sacc. Syll. Fung. 7: 176. 1888; Lloyd, Myc. Notes 67: 1142. 1922.

Illustrations: Payer, Bot. Crypt. 114, *f.* 527; Quélet, Mém. Soc. d'Émulation de Montbéliard 4: *pl.* 4, *f.* 2 [often cited as Champ. du Jura et des Vosges 2: *pl.* 4, *f.* 2]; Roumeguère, Cryptog. Illustr. *f.* 376; Tulasne, Ann. Sci. Nat. Bot. II. 19: *pl.* 17, *f.* 20; Fung. Hypog. *pl.* 21, *f.* 2.

Type: in Tulasne Herb. at Paris and in Broome Herb. at British Museum.

Fructifications the size of a filbert, globose, regular, somewhat soft, with a minute absorbing base; fibrils absent; peridium membranaceous, smooth, white, at length becoming light yellow, rimose, not separable, 80–90  $\mu$  thick, of very slender, densely tangled hyphae; gleba light ochraceous; cavities small, usually empty; septa thin, 12–15  $\mu$  thick, homogeneous, of gelified hyphae, not scissile; basidia 2–3-spored, rarely 4-spored, cylindrical; cystidia narrower, elongate-conical; spores hyaline, more deeply colored with age, becoming fuscous, 6.5–8.5  $\mu$  in diameter, spines short, sometimes appendiculate.

Almost epigeous. Solitary in shady stands of *Carpinus*. Italy and France.

ITALY: Lucca, C. E. Broome (Brit. Mus.).

FRANCE: Vienne, Couhe-Verac, Tulasne, Oct. 1841, type (Paris and Brit. Mus.); Doubs, Hérimoncourt, L. Quélet (Upsala); Jura, L. Quélet (Upsala).

7. *SCLEROGASTER SICULUS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 371. 1935.

*Sclerogaster lanatus* Mattiolo, Malpighia 14: 85–86. 1900. —non Hesse, Hypog. Deutschl. 1: 84. 1891.

Type: in Mattiolo and Dodge Herb. and Lloyd Museum.

Fructifications 0.6  $\times$  0.4 cm., depressed-globose, white, floccose; peridium duplex, the outer layer variable in thickness, composed of slender, thick-walled hyphae entangling soil particles, inner layer about 90  $\mu$  thick, composed of densely woven, periclinal hyphae; gleba ochraceous-tawny, hard; cavities filled with spores; septa about 30  $\mu$  thick between hymenia; basidia evanescent; spores brown, thick-walled, sparsely and minutely echinate, 4.1–5.6  $\mu$ .

Sicily, known only from the type locality.

SICILY: Fanfani & Cefalu, O. Mattiolo, 4 Apr. 1900, type (Lloyd Mus. and Dodge).

8. *SCLEROGASTER MINOR* Coker & Couch, Gast. Eastern U. S. & Canada, 25-26. 1928.

Illustrations: Coker & Couch, Gast. Eastern U. S. & Canada, pl. 17, 18, 106.

Type: in Herb. Univ. North Carolina.

Fructifications depressed-globose,  $0.3-1.0 \times 0.3-0.7$  cm., more or less covered with a cottony mycelium, white; peridium  $300-450 \mu$  thick, drying  $140 \mu$ , with a thin, cottony outer layer and a thick, pseudoparenchymatous inner layer, easily separable; gleba white, becoming deep ochraceous-yellow, with suggestions of a columella; cavities minute, filled with spores; septa  $60-185 \mu$  thick, composed of septate hyphae  $3-5 \mu$  in diameter; basidia long, cylindrical,  $28-40 \times 4-7.4 \mu$ , 1-5-spored; spores  $7.4-9.5 \mu$  in diameter, spherical, smooth at first, becoming warted.

Under *Juniperus*. North Carolina. August.

NORTH CAROLINA: Chapel Hill, J. N. Couch 7474, type (Univ. N. Car. Herb.).

9. *SCLEROGASTER LIOSPERMUS* (Tulasne) Soehner, Krypt. Forsch. 1: 393. 1924.

*Hydnangium liospermum* Tulasne, Fung. Hypog. 76. 1851; DeToni in Sacc. Syll. Fung. 7: 176. 1888; Hesse, Hypog. Deutschl. 1: 84. 1891; Zeller & Dodge, Ann. Mo. Bot. Gard. 11: 407-408. 1924.

*Octaviania liosperma* Lloyd, Myc. Notes 67: 1141. 1923.

Illustrations: Tulasne, Fung. Hypog. pl. 21, f. 1.

Type: in Tulasne Herb. at Paris.

Fructification size of a pea, firm, spherical, white, with a slight sterile base, here and there enveloped in a white-floccose mycelium, separating in places; peridium about  $180 \mu$  thick, not separable, homogeneous, of peridinal hyphae embedded in a gel, continuous with the septa; gleba firm, light ochraceous to apricot-color; cavities unequal in size, narrow, oblong, radiating from the center to the periphery; septa cartilaginous, gray, variable in thickness, those arising from the base much thicker than the others; spores borne terminally, mostly on short sterigmata, spherical,  $6-7 \mu$  in diameter, smooth or nearly so, rather thick-walled.

Under fallen leaves in oak woods. France. Autumn.

FRANCE: Loiret, Gien, Parc de Beauvoir, *Tulasne*, type (Paris).

10. *SCLEROGASTER COMPACTUS* (Tulasne) Saccardo, Syll. Fung. 11: 170. 1895.

*Octaviania compacta* Tulasne, Giorn. Bot. Ital. 1<sup>2</sup>: 55. 1844; Fung. Hypog. 79. 1851; DeToni in Sacc. Syll. Fung. 7: 160. 1888; Lloyd, Myc. Notes 67: 1142. 1922, in part.

*Hydnangium compactum* Quélet, Ench. Fung. 247. 1886. —not Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 250. 1899.

*Octavianina compacta* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

Illustrations: Tulasne, Fung. Hypog. *pl.* 11, *f.* 3.

Type: in Berkeley Herb. at Kew, Broome Herb. at British Museum, and Tulasne Herb. at Paris.

Fructifications small, spherical, drying about 6 mm. in diameter, covered by a loose, flocculent mycelium; columella penetrating to the center of the fructification or a little beyond; peridium 120–140  $\mu$  thick, not separable, of large, loosely tangled, thin-walled hyphae; gleba cinnamon-buff, texture very hard as in *Leucogaster*; cavities filled with spores; septa thin, about 15  $\mu$  thick between hymenia, composed of more or less periclinal, thick-walled hyphae embedded in a gel; basidia evanescent; spores spherical, sparsely and minutely warted, thick-walled, 4–6  $\mu$  in diameter.

FRANCE: Var, Hyères, *Tulasne*, 1844, 1845, type (Kew, Brit. Mus., and Paris); Provence, *E. Boudier*, 1900 (Paris).

#### MACCAGNIA

*Maccagnia* Mattiolo, R. Accad. Naz. dei Lincei. V. 13<sup>12</sup>: 13–17. 1922; E. Fischer in Engler & Prantl, Die Nat. Pflanzenfam. ed. 2, 7a: 23. 1933.

The type species of the genus is *Maccagnia carnica* Mattiolo.

Fructifications small, spherical, drying hard and horny; columella highly developed; lactiferous ducts abundant; cavities filled with small hyaline, thick-walled spores on zig-zag hyphae, as in *Leucogaster* and *Leucophlebs*, which soon form a gel in

which the basidia and spores are later borne; spores spherical with a thick epispore, rather small, echinate.

This genus seems intermediate between *Sclerogaster*, *Leucogaster*, and *Arcangeliella*, having the spores and texture of a *Sclerogaster*, the general ontogeny of a *Leucogaster*, and the columella and lactiferous ducts of an *Arcangeliella*. It will be remembered that *Sclerogaster compactus* and *S. luteocarneus* have a more or less well-developed columella but in all other characters seem closer to *Sclerogaster* than to *Maccagnia*. So far this genus is known from a single collection from Italy.

*MACCAGNIA CARNICA* Mattirol, R. Accad. Naz. dei Lincei. V. 13<sup>12</sup>: 13-17. 1922.

Illustrations: R. Accad. Naz. dei Lincei. V. 13<sup>12</sup>: pl. 1.

Type: Probably in Mattirol Herb., a portion in Patouillard Herb. at Farlow Herb.

Fructifications small, 0.8-1.0 cm. in diameter, spherical, sometimes attenuate at the base, becoming horn-like when dry, isabelline-yellow to isabelline-umber; peridium 120-150  $\mu$  (mean 125  $\mu$ ) thick, composed of very slender periclinal hyphae with very abundant, varicose, tortuous, moniliform, lactiferous ducts filled with a transparent yellow substance; columella branched, forming the veins; gleba chestnut-color; cavities radially arranged, somewhat circular, at first filled with small, hyaline, thick-walled spores 3-4  $\mu$  in diameter borne on zig-zag hyphae; septa thin, of highly gelified hyphae with lactiferous ducts; basidia clavate on a long pedicel, gelifying early, 4-, rarely 2-spored, sterigmata filiform; spores spherical, slightly appendiculate, epispore relatively thick, yellow-greenish, 4-5  $\mu$ , occasionally 6  $\mu$ , in diameter.

ITALY: Udine, Gemona, *Maccagnia* (Mattirol Herb. and Farlow).

#### HYDNANGIUM

*Hydnangium* Wallroth in Dietrich, Fl. Reg. Boruss. [Fl. Königr. Preuss.] 7: no. 465. 1839; Corda, Anleit. z. Stud. Myc. 114, lxxxiii. 1842; Icon. Fung. 5: 28. 1842; Tulasne, Ann. Sci. Nat. Bot. II. 19: 376. 1843; Fung. Hypog. 74. 1851; Rabenhorst, Deutschl. Krypt.-Fl. 1: 249. 1844; Fries, Summa Veg.

Scand. 436. 1849; Berkeley, *Outlines Brit. Fungol.* 293. 1860; Winter in Rabenhorst, *Krypt.-Fl. Deutschl.* ed. 2. 1: 877. 1883; Quélet, *Ench. Fung.* 247–248. 1886; DeToni in Sacc. *Syll. Fung.* 7: 175–177. 1888; Hesse, *Hypog. Deutschl.* 1: 81–84. 1891; E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam. I.* 1<sup>st</sup>: 310. 1899; and ed. 2, 7a: 30–31. 1933; Hollós, *Magyar. Földalatti Gombai*, 96–97, 207–208. 1911.

*Martellia* Mattirollo, *Malpighia* 14: 78–82. 1900; Saccardo & Sydow in Sacc. *Syll. Fung.* 16: 252. 1902.

*Octaviania* Auct. (pro parte) especially Lloyd, *Myc. Notes* 7: 1138–1142. 1922 (for discussion of nomenclature see *Ann. Mo. Bot. Gard.* 23: 603–604. 1936).

The type species of the genus is *Hydnangium carneum* Wallroth. The type species of *Martellia* is *M. mistiformis* Mattirollo. The type species of *Octaviania*, as used by authors subsequent to Tulasne including Lloyd, is *O. asterosperma* Vitt.

Fructifications spherical to slightly irregular, without sterile base or columella; peridium filamentous or prosenchymatous, rarely pseudoparenchymatous, more or less uniform in texture, without lactiferous ducts; gleba often fragile as in *Hymenogaster*, usually light-colored; basidia mostly 4- or 2-spored, usually projecting beyond the general level of the hymenium at maturity; spores spherical or nearly so, echinate, often with long slender spines not alveolate, or with ridges as is frequently the case in *Arcangeliella*.

Various characters have been used to separate this genus from the genus *Arcangeliella*. The early authors emphasized the presence or absence of sterile base, referring here species without one, and to *Octaviania* those with a well-developed one. While this character may be of some theoretical importance from the standpoint of developmental morphology it is very difficult to apply, as in very few species does the sterile base persist to full maturity, with a result that immature specimens were apt to be referred to *Octaviania* and very mature ones to *Hydnangium*. In the present treatment this practice has been followed, but it has not been used as a key character, as other characters are easier to apply. In the latter part of the last century, ease of dehiscence of the peridium was used.



Again this character is difficult to apply, as so many variations occur and too often the peridium is partly lacking rather as an accident to the individual specimens than because of any morphological character. In general, the species with a separable peridium are referable to *Arcangeliella* and those with a more persistent peridium remain in *Hydnangium*. An important exception is *H. mistiforme* Matt. which was segregated by Mat-tiolo chiefly on this character as *Martellia*. The spores are also brown rather than hyaline. Neither character seems sufficiently important to us to warrant generic segregation in the light of our present knowledge of the group. Lloyd, Myc. Notes 7: 1139-1142. 1922, redefined *Arcangeliella* as having a gleba "hard cartilaginous (horny when dry), hard to cut" including the type species *A. Borziana* Cav. and *A. luteo-carnea* (Bres.) Lloyd, the latter species here treated as *Sclerogaster* although slightly aberrant in that genus. All the other echinulate and alveolate species were referred to *Octaviania*. Hardness of the gleba seems to us an accidental character, dependent partly on the thickness of septa, their state of gelification, and method or care in drying.

## KEY TO SPECIES OF HYDNANGIUM

1. Peridium duplex..... 2
1. Peridium simplex, without pseudoparenchyma..... 5
  2. Pseudoparenchyma present in one layer of peridium..... 3
  2. Pseudoparenchyma absent; spores dark brown..... 4
3. Spores dark brown.....1. *H. citrinum* (p. 577)
3. Spores hyaline.....2. *H. monticola* (p. 578)
  4. Spores 6-8  $\mu$  in diameter; peridium 300  $\mu$  thick.....3. *H. Eisentii* (p. 578)
  4. Spores 10-13  $\mu$  in diameter; peridium thinner.....4. *H. laeve* (p. 579)
5. Spores hyaline or nearly so..... 6
5. Spores brown..... 12
  6. Spores 5-6  $\mu$  in diameter.....5. *H. compactum* (p. 580)
  6. Spores 7.4-9  $\mu$  in diameter.....6. *H. Parksii* (p. 580)
  6. Spores mostly over 20  $\mu$  in diameter, echinulate, spines 3-3.5  $\mu$  long  
.....7. *H. Gilkeyae* (p. 581)
  6. Spores 10-20  $\mu$  in diameter..... 7
7. Peridium white, 400  $\mu$  thick.....8. *H. album* (p. 581)
7. Peridium pinkish or reddish..... 8
7. Peridium yellow or brownish..... 9
  8. Peridium 30-40  $\mu$  thick.....9. *H. pila* (p. 582)
  8. Peridium 110-120  $\mu$  thick..... 10a. *H. carneum* var. *purpureum* (p. 584)
  8. Peridium 150-270  $\mu$  thick.....10. *H. carneum* (p. 582)

9. Sterile base prominent, hemispheric, stipe short, slender; peridium 200  $\mu$  thick.....11. *H. pusillum* (p. 585)
9. Sterile base not prominent..... 10
10. Peridium thick, 1200–1300  $\mu$ .....12. *H. luteolum* (p. 585)
10. Peridium 150–230  $\mu$  thick..... 11
10. Peridium 110–120  $\mu$  thick.....10a. *H. carneum* var. *purpureum* (p. 584)
10. Peridium 60–80  $\mu$  thick.....13. *H. Archeri* (p. 586)
10. Peridium thin, septa thick.....14. *H. aurantiacum* (p. 586)
11. Spores 15–16  $\mu$  in diameter.....15. *H. monosporum* (p. 587)
11. Spores 8.5–12  $\times$  11–14  $\mu$ .....16. *H. aurantium* (p. 588)
12. Spores 6–10  $\mu$  in diameter..... 13
12. Spores 10–20  $\mu$  in diameter..... 14
13. Peridium separable, white-olivaceous.....17. *H. mistiforme* (p. 588)
13. Peridium not separable, capucine-yellow or pink.....18. *H. Thaxteri* (p. 589)
14. Peridium white, changing to deep vinaceous, drying vinaceous, 500–600  $\mu$  thick.....19. *H. purpureum* (p. 589)
14. Peridium white, changing to dark brown on exposure, about 300  $\mu$  thick.....20. *H. Hessei* (p. 590)
14. Peridium white, unchanging, 600–700  $\mu$  thick.....21. *H. lanigerum* (p. 591)
14. Peridium pale flesh-color, 140  $\mu$  thick.....22. *H. javanicum* (p. 592)
14. Peridium brownish..... 15
14. Peridium black, 260–270  $\mu$  thick.....23. *H. nigricans* (p. 592)
15. Peridium thick, 900–1000  $\mu$ .....24. *H. tuberculatum* (p. 593)
15. Peridium 400–500  $\mu$  thick; Australia.....25. *H. densum* (p. 593)
15. Peridium 300–400  $\mu$  thick, auburn or chestnut.....26. *H. luteum* (p. 594)
15. Peridium 50–60  $\mu$  thick, dark brown to black.....27. *H. Soehneri* (p. 595)
15. Peridium 40–50  $\mu$  thick, waxy yellow drying tawny.....28. *H. cereum* (p. 595)

1. *HYDNANGIUM CITRINUM* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 371. 1935.

*Octaviania citrina* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 252. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 248–249. 1902.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications depressed-globose to irregular, 1.3  $\times$  2 cm., white becoming ochraceous-tawny in alcohol, dirt clinging to the peridium in spots; peridium duplex, 200  $\mu$  thick, the outer portion of strands of parallel hyphae which grow outward and entangle dirt, with pseudoparenchyma of large cells within; gleba orange, becoming ochraceous-tawny in alcohol; cavities empty; septa 70–80  $\mu$  thick, composed of pseudoparenchyma with cells 10–11  $\mu$  in diameter; basidia clavate, 4-spored, 20  $\times$  11  $\mu$ ; sterigmata 6–7  $\mu$  long with slightly swollen bases; spores

spherical, echinulate, pedicellate, yellow-brown, 10–12  $\mu$  in diameter.

Under *Arctostaphylos glaucus*. California. April.

The cotypes in the Dudley Herbarium have no data associated with them other than the numbers on the bottles and the names which Harkness gave them. Harkness mentions three localities in his original description and there are three bottles labeled *Octaviania citrina* in the Dudley Herb. Two of them belong clearly to this species, while the third, of very different structure although of much the same color, seems to be discolored specimens of *H. carneum*. Harkness cites as his localities: Oat Hill Quicksilver Mine, Solano County; Camp Taylor, Marin County; and Calistoga, Napa County.

CALIFORNIA: *H. W. Harkness 155b, 157, cotype* (Stanford).

2. *HYDNANGIUM MONTICOLA* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

*Octaviania monticola* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 254. 1899. Saccardo & Sydow in Sacc. Syll. Fung. 16: 248. 1902.

Illustrations: Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: *pl. 42, f. 3*.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications irregular, 2  $\times$  3  $\times$  3 cm., flexible, buff, becoming Verona brown in alcohol; sterile base prominent, no columella; peridium duplex, 300  $\mu$  thick, the outer layer up to 100  $\mu$  thick, composed of thin-walled, slender, hyaline hyphae, the inner layer pseudoparenchymatous; gleba a little lighter than the peridium, spongy; cavities empty; septa hyaline, 80–120  $\mu$  thick, of rather indefinite structure resembling the outer peridium; basidia clavate, 35  $\times$  6–7  $\mu$ , 4-spored; sterigmata short; spores 10–12  $\mu$  in diameter, minutely verrucose.

Mountain regions in sandy soil. California. April.

CALIFORNIA: Placer County, Auburn, *H. W. Harkness 13*, cotype (Stanford); Santa Clara County, Alma, *H. E. Parks 404* (Univ. Cal. and Zeller).

3. *HYDNANGIUM EISENII* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 371. 1935.

*Melanogaster Eisenii* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 259. 1899.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications 1.5 cm. in diameter, brown becoming russet to clay-color in alcohol; peridium about 500–600  $\mu$  thick, composed of very slender, thin-walled, compactly woven hyphae, with clamp connections, frequently ending in pyriform bodies, but composing a single, hyaline, homogeneous layer, with a dark brown surface of the same texture, about 7  $\mu$  thick; gleba dark brown; cavities densely crowded with spores; septa brownish, soon disappearing, composed of small, gelified, interwoven hyphae; basidia inconspicuous,  $25 \times 7 \mu$ ; sterigmata long; spores brown, globose, echinate, 6–8  $\mu$  in diameter.

Lower California. January.

MEXICO: Baja California, Cabo S. Lucas, *G. Eisen*, cotype (Harkness 116, Stanford, and histological slide of a fragment in Zeller).

4. *HYDNANGIUM LAEVE* (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

*Octaviania laevis* Hesse, Hypog. Deutschl. 1: 80–81. 1891.

*Octavianina laevis* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Octaviania levis* Saccardo, Syll. Fung. 11: 169. 1895.

*Arcangelhiella laevis* (Hesse) Dodge, Ann. Mo. Bot. Gard. 22: 368. 1935.

Illustrations: Hesse, Hypog. Deutschl. 1: *pl. 7, f. 15–17*.

Type: location unknown to us but authentic material in Herb. Bot. Inst. Univ. Marburg.

Fructifications spherical, 1.5 cm. in diameter, smooth, white then russet to almost black in alcohol; peridium thin, duplex, outer layer sloughing off leaving patches composed of septate hyphae, inner layer 30–40  $\mu$  thick, stupose, brownish-yellow, composed of closely woven, gelified hyphae, becoming smaller next the gleba; gleba white becoming yellowish and finally Sudan brown in alcohol, cavities small and long, soon filled with spores; septa very thin, later yellowish, composed of compactly woven, gelified hyphae 2  $\mu$  in diameter; basidia clavate, short, paraphyses shorter; sterigmata as long as the diameter of the mature spore or longer; spores colorless, becoming yellowish-brown, 10–13  $\mu$  in diameter, with large blunt spines.

Under birch. Hessen-Nassau, Germany, and Oregon. July to September, mostly in August.

The specimen studied was collected in the type locality twelve years later than the original specimen but three years before the species was described and was determined by Hesse.

GERMANY: Hessen Nassau, Altmorschen, *R. Hesse*, VII/88; Auc. *R. Hesse*, V/89 (both Hesse and Dodge).

OREGON: Marion County, Salem, *S. M. Zeller 2186* (Zeller).

5. *HYDNANGIUM COMPACTUM* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 250. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 255. 1902.—*not* Quélet, Ench. Fung. 247. 1886.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructification depressed-globose, 2 cm. in diameter, white becoming Sayal brown to tawny-olive in alcohol; peridium 120–130  $\mu$  thick, composed of hyaline, slender, compactly woven, gelified hyphae; gleba light ochraceous-buff, cavities empty; septa 80  $\mu$  thick, composed of hyaline, slender, compactly woven gelified hyphae; basidia oblong,  $20 \times 4-5 \mu$ , sterigmata short; spores very sparsely echinulate, with very small spines, 5–6  $\mu$  in diameter.

Under *Ceanothus*. California and Australia. May to June.

CALIFORNIA: Placer County, Auburn, *H. W. Harkness 191*, type (Stanford); Santa Clara County, *H. E. Parks 1000* (Univ. Cal., Dodge, and Zeller); Guadalupe, *H. E. Parks 153, 422, 801* (Univ. Cal., Dodge, and Zeller); Alma, *H. E. Parks 163a* (Univ. Cal., Dodge, and Zeller 1638).

AUSTRALIA: S. Australia, *J. B. Cleland 2* (Cleland and Dodge).

6. *HYDNANGIUM Parksii* Zeller & Dodge, sp. nov.

Fructificationes magnae, 2–3 cm. diametro metientes, sphaericae, albae, fulvae conservatae, superficie glabra, basis sterilis columellaque non visae; peridium ad 640  $\mu$  crassitudine, hyphis subpericlinalibus dense contextum; gleba alba, “ochraceous buff” conservata, locellis parvis; septa 65–70  $\mu$  crassitudine, hyphis dense contexta; basidia cylindrica, bispora,  $22 \times 6-7 \mu$ ; sporae 7.4–9  $\mu$ , hyalinae, minute echinulae.

Type: in Univ. Cal. Herb.

Fructifications large, 2–3 cm. in diameter, spherical, white becoming tawny in alcohol, surface smooth, no sterile base nor columella present; peridium up to 640  $\mu$  thick, composed of

densely woven, more or less periclinal hyphae; gleba white becoming ochraceous-buff in alcohol; cavities small; septa about  $65\text{--}70\ \mu$  thick, of compactly woven, thin-walled hyphae; basidia cylindric, 2-spored,  $22 \times 6\text{--}7\ \mu$ ; spores  $7.4\text{--}9\ \mu$  in diameter, minutely echinulate, hyaline.

It is possible that this is still immature, in which case the thickness of the peridium and of the septa as given above is probably too great and the spore markings too minute.

CALIFORNIA: Santa Clara County, Guadalupe, *H. E. Parks 521* (Univ. Cal.).

7. *HYDNANGIUM GILKEYAE* Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 371. 1935.

Type: in Oregon State Agr. Coll., Dodge, and Zeller Herbaria.

Fructifications oblong to subspherical, about  $4.5 \times 3 \times 3\text{ cm.}$ , brittle; surface glabrous with innate reticulate veins, buff with brownish stains, drying pinkish-buff to tawny-olive, with the veins slightly darker; no sterile base showing in youngest specimens seen (1 cm. broad); peridium  $150\text{--}200\ \mu$  thick, drying  $70\text{--}85\ \mu$ , of hyaline prosenchyma, appearing finely stipose when dried; gleba white to slightly creamy when fresh, drying pale orange-yellow to maize-yellow; cavities medium size; septa cream-color, hyaline *sub lente*, of loosely interwoven, large hyphae, scissile at angles,  $35\text{--}40\ \mu$  thick; basidia 1-2-spored, clavate, protruding beyond the paraphyses; spores large, subspherical, mostly longer than broad, yellowish-brown, with large echinulae about  $3\text{--}3.5\ \mu$  long, pedicellate,  $18\text{--}22 \times 14.5\text{--}8.5\ \mu$  including the spines, episore  $0.7\text{--}1.0\ \mu$  thick.

Hypogaeous, under *Corylus californicus*. Oregon. May.

OREGON: Linn County, near the Peoria Road, *Helen M. Gilkey*, type (Oregon State, Dodge, and Zeller 2334).

8. *HYDNANGIUM ALBUM* Harkness, *Proc. Cal. Acad. Sci. Bot.* III. 1: 251. 1899; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 255. 1902.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications spherical, 1 cm. in diameter, dirty white becoming brownish in alcohol; peridium simplex,  $400\ \mu$  thick, composed of hyaline, slender, closely woven, branched hyphae;

gleba ochraceous; cavities minute, empty; septa  $75\ \mu$  thick, composed of hyaline, slender, closely woven, branched hyphae; basidia clavate,  $20 \times 6\ \mu$ , sterigmata  $6\text{--}7\ \mu$  long; spores dilute yellowish, minutely reticulate with short sharp spines,  $11\text{--}15\ \mu$  in diameter.

In the forest. California. Spring.

In the outer part of the peridium and in the tramal tissues are dark brown bodies resembling latex organs, but the species has not been referred to *Arcangeliiella* since no columella was reported in the type.

CALIFORNIA: Napa County, Calistoga, *H. W. Harkness 178*, cotype (Stanford).

9. *HYDNANGIUM PILA* Patouillard, Bull. Soc. Myc. France 26: 201. 1910; Saccardo & Trotter in Sacc. Syll. Fung. 21: 495. 1912.

Illustrations: Patouillard, Bull. Soc. Myc. France 26: 202, f. 2. 1910.

Type: Patouillard Herb. at Farlow Herb.

Fructifications depressed-globose to irregular, 2–3 cm. in diameter, white, reddening in air; peridium continuous above, often lacunose below, puberulent due to hyaline, cylindric cells of hyphae,  $30\text{--}40\ \mu$  thick, dense and tenacious near the gleba, easily separable, mycelium white, fibrous, little developed; gleba firm, white, then reddish; no sterile base; septa composed of slender, cylindric filaments supporting a pseudoparenchymatous subhymenial layer; basidia obtuse and rounded at the summit, rapidly attenuated below into a cylindric portion,  $30\text{--}35 \times 15\text{--}20\ \mu$ , 4-spored, sterigmata short, pointed; spores colorless, later very pale tawny, spherical to slightly ellipsoid,  $10\text{--}12\ \mu$  in diameter or  $10\text{--}14 \times 9\text{--}11\ \mu$ , echinulate, with a large oil drop.

Semi-hypogeous in oak woods. Central Europe. August.

GERMANY: Bayern, Euharting, *E. Soehner* (Soehner and Dodge).

FRANCE: Jura, Lépimay, *N. Patouillard*, type (Farlow).

10. *HYDNANGIUM CARNEUM* Wallroth in Dietrich, Fl. Reg. Boruss. [Fl. Königr. Preuss.] 7: no. 465. 1839; Tulasne, Fung. Hypog. 75. 1851; Winter in Rabenhorst, Kryptog.-Fl. Deutschl. ed. 2. 1: 877. 1883; DeToni in Sacc. Syll. Fung. 7: 175–176.

1888; Masee, Ann. Bot. 4: 37. 1889 [often cited as Monogr. Brit. Gast.]; Hesse, Hypog. Deutschl. 1: 82-83. 1891; Boudier, Icones Myc. 4: 98. 1905-1910; Th. M. Fries, Svensk Bot. Tidskr. 3: 273-274. 1909; Hollós, Magyar. Földalatti Gombai, 97. 207-208. 1911; Th. C. E. Fries, Ark. f. Bot. 17<sup>o</sup>: 12. 1922; Bataille, Bull. Soc. Myc. France 39: 192. 1923; ? E. Fischer, Geobot. Inst. Rübel in Zürich, Veröffentl. 3: 576-578. 1925.

*Octaviania carnea* Corda, Icones Fung. 6: 36. 1854; Lloyd, Myc. Notes 67: 1139-1140. 1922, in part.

?*Octaviana carnea* Rodway, Papers & Proc. Roy. Soc. Tasmania 1923: 157. 1924; ?Verwoerd, S. Afr. Jour. Sci. 22: 164. 1925.

*Octaviania ? mollis* De Notaris, Comment. Soc. Crittog. Ital. 1: 33. 1861; DeToni in Sacc. Syll. Fung. 7: 160. 1888.

*Octavianina mollis* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

Illustrations: Boudier, Icones Myc. 1: pl. 192; Bucholtz, Матеріалы къ морфологіи и систематицѣ подземныхъ грибовъ . . . Издап. Естеств. Ист. Музея Графини Е. П. Шереметевой въ с. Михайловскомъ Московской Губ. 1: pl. 4, f. 27-28; Corda, Anleit. z. Stud. Myc. pl. D, f. 47: 11-13; Icones Fung. 6: pl. 7, f. 66; DeBary, Vergl. Morphol. d. Pilze, ed. 2, 67, f. 28; P. Hennings, Verh. Bot. Ver. Prov. Brandenburg 40: pl. 1, f. 18; Hesse, Hypog. Deutschl. 1: pl. 2, f. 18-19; pl. 5, f. 16; Istvanffi, Ber. Deutsch. Bot. Ges. 13: pl. 37, f. 49; Masee, Ann. Bot. 4: pl. 1, f. 14; Nees von Esenbeck, Th. & A. Henry, Syst. d. Pilze 1: pl. 37, f. 1-6; Petri, Rendic. Cong. Bot. Palermo, 148-149; Nuovo Giorn. Bot. Ital. N. S. 9: pl. 14; Roumeguère, Cryptog. Illustr. f. 371b; Ruhland, Bot. Zeit. 59: pl. 7, f. 25-30; Tulasne, Fung. Hypog. pl. 21, f. 3; Van Bambeke, Mem. Acad. Roy. Belg. 54: pl. 1-3.

Type: Bot. Mus. Berlin, Kew, and Paris. The type distribution of *Octaviania mollis* De Notaris in Erb. Critt. Ital. 1052.

Fructifications spherical or oblately spheroidal, pale flesh-color, smooth; no columella nor sterile base seen; peridium 150-270  $\mu$  thick, compact, fibrous, stipose; gleba very pale, drying brownish, brittle, cavities irregular, medium size; septa 20-28  $\mu$  thick between hymenial layers, about 55  $\mu$  to tops of paraphyses, stipose, composed of slender gelified hyphae;



basidia 2-spored, projecting above hymenium,  $18-20 \times 10-13 \mu$ ; sterigmata  $5-6 \mu$  long; cystidia large, smooth, hyaline; spores spherical, echinulate (echinulae plus exospore about  $3 \mu$ ), averaging 16 echinulae on median limb of circle, dilute honey-colored *en masse*, hyaline singly,  $9.5-14 \mu$  in diameter (averaging about  $16 \mu$  including echinulae).

Europe and America. October.

There is a trace of a sterile base in Rabenhorst, Fung. Eur. 675.

EXSICCATI: Erb. Critt. Ital. 1052, under *Octaviania mollis*; Rabenhorst, Fung. Eur. 675; Herb. Viv. Myc. 1318; Sydow, Mycoth. Marchica, 3726; de Thümen, Mycoth. Univ. 109.

FINLAND: Helsingfors, Bot. Gard., *W. Nylander* (Paris).

SWEDEN: Upsala, *Th. M. Fries & R. Fries*, in Rabenhorst, Fung. Eur. 675 (copy in Farlow); Bot. Trädgård, *Th. M. Fries*, 1866 (Upsala).

GERMANY: Schlesien, *L. Becker*, in de Thümen, Mycoth. Univ. 109 (Lloyd Mus. and Mo. Bot. Gard.); Brandenburg, Grünwald, *F. Klotzsch*, type (Berlin, Kew, and Paris); Berlin, *P. Hennings*, in Sydow, Mycoth. Marchica, 3726 (copies in Farlow, Lloyd Mus. 0234, and another specimen with same date, Lloyd Mus. 4149, and Dodge, also as *v. caldariorum*, Berlin); *Klotzsch* (Kew); Bayern, Wolftratshaus, *E. Soehner 724* (Soehner, Berlin, and Dodge).

AUSTRIA: Niederösterreich, Schneeberggebiet, *F. von Hoehnelt* (von Hoehnelt Herb. B2603 at Farlow).

ITALY: Trentino, *G. Bresadola*, Nov. 1894 (Upsala); Genova, *F. Baglietto*, in Erb. Critt. Ital. 1052, under the name *Octaviania mollis* De-Notaris, type? (copies in Farlow and Lloyd Mus.); Roma, *O. Mattiolo* (Lloyd Mus.).

FRANCE: Alpes Maritimes, Antibes, *Poirault* (Farlow, Lloyd Mus. 6039, and Dodge); Golfe Jouan, *L. Eolland*, Feb. 1900 (Paris).

HOLLAND: Amsterdam, *Oudemans 307* (Upsala).

SCOTLAND: Glasgow Botanical Garden, *Dickson*, Oct. 1873 (Berkeley Herb. at Kew); Edinburgh (M. C. Cooke Herb. at Kew).

PORTUGAL: Lisbon, *C. Torrend*, Dec. 1907 (Paris as *f. minor*).

MASSACHUSETTS: Cambridge, *H. von Schrenk* (Mo. Bot. Gard. 1607); *H. Webster* (Farlow).

OREGON: Benton County, Corvallis, *S. M. Zeller 2566*; Linn County, Peoria, *S. M. Zeller 2588* (both Zeller).

CALIFORNIA: Alameda County, Berkeley, *E. A. Harper*, 3 collections (N. Y. Bot. Gard.); *Dale Parks & H. E. Parks 390* (Univ. Cal., Dodge, and Zeller); Santa Clara County, Saratoga, *H. E. Parks 496* (Univ. Cal.); Alma, *H. E. Parks 210, 152* (Univ. Cal., Dodge, and Zeller); Guadalupe Mines, *H. E. Parks 435* (Univ. Cal., Dodge, and Zeller).

JAMAICA: Cinchona, *W. A. & Edna L. Murrill 498* (N. Y. Bot. Gard. and Dodge).

URUGUAY: Montevideo, Miguelete, *G. Herter 86821* (Dodge).

10a. var. *PURPUREUM* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 78. 1919.

Type: At Peradeniya and Kew Herbaria.

Fructification  $1.0 \times 0.7$  cm., reniform, drying wrinkled, fawn-color to Natal brown; peridium 110–120  $\mu$  thick, stupose, composed of gelified strands of dark brown hyphae as in *H. Archeri*; gleba tawny-olive to isabella-color, cavities large, empty; septa 20  $\mu$  thick between hymenia, of slender, compact hyphae; basidia soon collapsing and evanescent, sterigmata long; spores hyaline or nearly so, spherical, 10–11  $\mu$  in diameter, with slender, short spines about 24 per great circle.

Known only from the type locality.

The position of this variety is uncertain. In peridial characters it seems closer to *H. Archeri*, while its spores are suggestive of *H. carneae* or some species of *Arcangiella*.

Ceylon: Ilakgala, *T. Petck* 5180 type, 6438 (Peradeniya, Kew, and Dodge).

11. *HYDNANGIUM PUSILLUM* Harkness in Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

Type: in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications 1 cm. in diameter, cinnamon-brown; sterile base prominent, ending in a hemispherical knob at top and prolonged below into a short, slender stipe; peridium about 200  $\mu$  thick, composed of thin-walled, hyaline, parallel hyphae; gleba buckthorn-brown; cavities large, irregular, empty; septa 100  $\mu$  thick, composed of thin-walled, slender, hyaline hyphae, beginning to gelify; basidia broadly clavate, with two sterigmata 3–4  $\mu$  long; spores spherical, 15  $\mu$  in diameter, with prominent, long, slender spines.

CALIFORNIA: *H. W. Harkness* 282, type (Stanford).

12. *HYDNANGIUM LUTEOLUM* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 251. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 255. 1902.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications small, irregular, white turning brown; peridium 1200–1300  $\mu$  thick, composed of thin-walled, very slender, closely woven hyphae; gleba orange-yellow; cavities small, empty; septa 35–40  $\mu$  thick, composed of coarse, gelified hyphae; basidia pyriform, 35–40  $\times$  8  $\mu$ , sterigmata short; spores

spherical, 12  $\mu$  in diameter, with small short spines not very closely placed, pedicellate.

In somewhat sandy soil beneath *Libocedrus decurrens*. California. July.

CALIFORNIA: Placer County, Alta, *H. W. Harkness 100*, cotype (Stanford).

13. *HYDNANGIUM ARCHERI* (Berkeley) Zeller & Dodge, *Ann. Mo. Bot. Gard.* **22**: 371. 1935.

*Octaviania Archeri* Berkeley in J. D. Hooker, *Bot. Antarctic Voy. III. Fl. Tasmaniae* **2**: 263-265. 1859; DeToni in *Sacc. Syll. Fung.* **7**: 160. 1888; Cooke, *Handbook Austral. Fungi*, 246. 1892; Rodway, *Papers & Proc. Roy. Soc. Tasmania* **1911**: 25. 1912.

*Octavianina Archeri* O. Kuntze, *Rev. Gen. Pl.* **3**<sup>2</sup>: 501. 1898. Type: in Kew Herb.

Fructifications obovate, drying 7-8 mm. in diameter, chocolate to burnt umber, sterile base large (fide Berkeley); peridium highly gelified, thin, 60-80  $\mu$  thick, composed of interwoven strands of coarse, parallel hyphae; gleba deep olive-buff to dark olive-buff, hard, cartilaginous; cavities large, polygonal, empty; septa chocolate, cartilaginous, 30-40  $\mu$  thick, composed of slender, gelified, parallel, brown hyphae; basidia not evident on account of the collapse of the hymenium; spores spherical, with long slender equal spines 24 per great circle, 2-3  $\mu$  long, spores without spines 12-14  $\mu$  in diameter.

On sandy ground. Tasmania, Australia, and New Zealand.

Both Oregon specimens are too young for certain determination.

TASMANIA: *Archeri*, type (Kew); Hobart, *L. Rodway 118* (Kew), *087*, *1108* (Lloyd Mus. and Dodge).

SOUTH AUSTRALIA: Morialta, *J. B. Cleland 11* (Cleland and Dodge); Mt. Lofty, *J. B. Cleland 13* (Cleland and Dodge).

NEW ZEALAND: *Colenso 1480* (Kew); Invercargill, *J. B. Cleland 9* (Cleland and Dodge).

OREGON: Benton County, Corvallis, *S. M. Zeller 7254* (Zeller); *H. P. Barsa* (Zeller 8183).

14. *HYDNANGIUM AURANTIACUM* Heim & Malençon, *Treb. Mus. Cienc. Nat. Barcelona* **15** [Ser. Bot. 3]: 69-74. 1934.

*Hydnangium carotaecolor* Codina & Font-Quer, *Cavanill.* **3**: 169-170. 1931.

Illustrations: Heim & Malençon, Treb. Mus. Cienc. Nat. Barcelona 15 [Ser. Bot. 3]: 70, f. 16.

Type: not seen by us, probably in Paris or Barcelona.

Fructifications 1.5–2 cm. in diameter, subspherical, wrinkled, rough, from yellow to orange (jaune orangé, K, Code 136, 141); peridium thin, arachnoid, absent in places, composed of yellow (Code 161) fibres; no columella or sterile base, although the base is provided with a tuft of rooting whitish or yellow fibrils, mycelium yellow; gleba dense, bright yellow (orange safrané, Code 131), cavities small, crowded; septa comparatively thick; basidia clavate, cylindric or obconic,  $38-40 \times 8-10 \mu$ , with 2–4 sterigmata  $3.5-4 \times 1.2-1.6 \mu$ ; spores spherical or somewhat obovate,  $11-16 \mu$  in diameter, with two walls and a thick epispore composed of terete, obtuse tubercles  $1.5 \mu$  long arranged singly or in rows or joined by an imperfect reticulum, pale yellow, often with remains of the sterigma  $3-4$  (–6)  $\mu$  long,  $2 \mu$  in diameter.

In wooded moist ravine facing north, under *Quercus Ilex*. Montserrat. October.

15. *HYDNANGIUM MONOSPORUM* Boudier & Patouillard, Jour. de Bot. [Morot] 2: 445. 1888; Patouillard, Tab. Anal. Fung. 7: 71. 1889; Saccardo, Syll. Fung. 9: 280–281. 1891; Boudier, Icones Myc. 4: 98–99. 1905–1910.

*Octaviania monospora* Lloyd, Myc. Notes 67: 1141. 1922.

Illustrations: Boudier, Icones Myc. 1: pl. 193; Patouillard, Tab. Anal. Fung. f. 692.

Type: cotype in Lloyd Museum.

Fructifications ovate-pyriform, irregularly depressed above, 3–4 cm. in diameter, ochraceous-tawny, somewhat papillate, squamulose at the surface; peridium  $150-220 \mu$  thick, composed of parallel, hyaline hyphae; gleba firm, white, becoming yellowish and tawny where wounded; cavities small, empty; septa  $30-50 \mu$  thick, composed of loosely interwoven, hyaline hyphae  $3-5 \mu$  in diameter; basidia oblong-clavate,  $30-40 \times 12 \mu$ , with a single long sterigma tapering above; spores brownish, spherical, minutely echinulate, appearing smooth under low power, appendiculate, uniguttulate,  $15-16 \mu$  in diameter; odor of pine-apples.

In clay soil. Germany and southern France.

GERMANY: Bayern, Munchen, *E. Soehner 1060* (Soehner and Dodge).

FRANCE: Nice, *J. Barla*, cotype (ex Boudier Herb. in Lloyd Mus. 5343, Dodge, Patouillard Herb. at Farlow, and Upsala, com. Bresadola sub *H. candidum*).

16. *HYDNANGIUM AURANTIUM* (Harkness) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 5: 30. 1918.

*Rhizopogon aurantius* Harkness, *Proc. Cal. Acad. Sci. Bot.* III. 1: 257. 1899; Saccardo, *Syll. Fung.* 16: 251. 1902.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications subspherical, solitary, 1-2 cm. in diameter, dirty white drying yellowish tawny to Mars brown, dark brown in alcohol; peridium 160-280  $\mu$  thick, homogeneous, of fine interwoven hyphae which become gelified at maturity, hyaline, with outer layer about 50-60  $\mu$  thick, of very compact, more or less erect, fine hyphae becoming brown; gleba orange when fresh, drying warm buff to ochraceous-buff or pale orange-yellow, cavities subglobose to irregular, empty; septa 30-60  $\mu$  thick, composed of slender hyphae, compactly interwoven, becoming scissile; basidia clavate, hyaline, 2-spored, 20-35  $\times$  8-10  $\mu$ , sterigmata 5-7  $\mu$  long; paraphyses cylindrical, septate; cystidia capitate with narrow necks, 48-52  $\times$  11-14  $\mu$ ; spores subglobose to obovoid, pediculate, 8.5-12  $\times$  11-14  $\mu$ , dilute olivaceous, finely echinulate-alveolate, exospore about 1-1.5  $\mu$  thick; odor pleasant as of certain polypores.

Hypogeous, in open coniferous woods. Western Washington, Oregon, and California. May to October.

This species is hunted by pine squirrels and other rodents.

WASHINGTON: Jefferson County, Quinalt, *C. A. Brown & C. H. Kauffman* (Univ. Mich. and Zeller).

OREGON: Benton County, 7 miles west of Alsea, *S. M. Zeller 1960* (Zeller); Coos County, Sunset Beach, near Cape Arago Lighthouse, *N. L. Gardner 408* (Univ. Calif., Dodge, and Zeller).

CALIFORNIA: Marin County, Mt. Tamalpais, *H. W. Harkness 74*, cotype (Stanford); Santa Clara County, Saratoga, *H. E. Parks 1142 & C. W. Dodge 1152* [immature] (Dodge).

17. *HYDNANGIUM MISTIFORME* (Mattiolo) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 372. 1935.

*Martellia mistiformis* Mattiolo, *Malpighia* 14: 78-82. 1900; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 252. 1902.

Illustrations: Mattiolo, *Malpighia* 14; *pl. 1, f. 1-4*.

Type: probably in Mattiolo Herb., a portion in Patouillard Herb. at Farlow. Herb.

Fructifications spherical and irregular, about 1 cm. in diameter, olivaceous-white; peridium smooth, easily separable, variable in thickness, composed of gelified compact hyphae, the outer ones enclosing grains of sand; gleba rather firm, umber to chestnut; cavities small, irregular, gyrose with a tendency to arise from the sterile base; septa cottony-filamentous, scissile; basidia short-cylindric, 35–40  $\mu$  long, arising from subhymenial pseudoparenchyma, 4-spored; sterigmata slender, 4–5  $\mu$  long; spores spherical or slightly ellipsoidal, about 10  $\mu$  in diameter, umber, slightly echinate.

ITALY: Sardinia, Orune, *U. Martelli*, type (Patouillard Herb. at Farlow).

18. *HYDNANGIUM THAXTERI* Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 372. 1935.

Type: in Farlow Herb. at Harvard Univ.

Fructifications spherical, color of crushed strawberries, drying capucine-yellow; columella scarcely more than thickened septum branching and disappearing in the middle of the fructification; peridium 125–130  $\mu$  thick, outer layer 30  $\mu$  thick, of closely woven, slender hyphae, and inner layer 100  $\mu$  thick, of larger, more loosely woven, periclinal hyphae; gleba orange-buff to light ochraceous-buff; cavities minute; septa 50–60  $\mu$ , of slender interwoven hyphae, subhymenium pseudoparenchymatous; basidia short-cylindric; sterigmata long; spores 7–8  $\mu$  in diameter, spherical, about 20–24 slender spines per great circle.

This species was found growing with *Rhizopogon occidentalis* under leaves on a dry hilltop above Concepción. Thaxter states "Color dirty cream running to crushed strawberry red." Since we have not seen *R. occidentalis* with more than pale pink tints, we have assumed that the deeper color mentioned applied to our species.

CHILE: Concepción, *E. Thaxter*, Nov. 1905, type (Farlow).

19. *HYDNANGIUM purpureum* (Coker & Couch) Zeller & Dodge, *comb. nov.*

*Octaviania purpurea* Coker & Couch, Gast. Eastern U. S. & Canada, 50. 1923.

Illustrations: Coker & Couch, Gast. Eastern U. S. & Canada, pl. 30, 31, 111.

Type: in Univ. North Carolina Herb., a portion in Dodge Herb.

Fructifications 0.6–2.5 cm. in diameter, drying 0.4–1.6 cm., oblately spheroidal to irregularly lobed, with branched rhizomorphs, white turning vinaceous to deep vinaceous on exposure or wounding, drying vinaceous, without sterile base or columella; peridium 1–2 mm. thick, drying 150–450  $\mu$  thick, separable, composed of slender, densely woven hyphae 3–4  $\mu$  in diameter, and a few much larger, thick-walled hyphae 11–16  $\mu$ , often ending in large spherical cells; gleba white at first becoming olive-brown to deep blackish-brown; septa white, 30–40  $\mu$  thick, of slender gelified hyphae with groups of cavities separated by much thicker septa; basidia 20–25  $\times$  7.4–11.2  $\mu$  when young, sending up an epibasidium 4.4–5.5  $\mu$  in diameter, bearing a single spore so that the mature basidium is flask-shaped, 30–44  $\times$  5.5–7.8  $\mu$  and early collapsing; spores broadly ellipsoidal, 9.5–12.5  $\mu$  in diameter, thick-walled, with large warts.

North Carolina. July and August.

The systematic position of this species is not clear, and it is with hesitation that we have referred it to *Hydnangium*. We have seen no trace of sterile base and columella. The large thick-walled hyphae of the peridium are very suggestive of lactiferous ducts, but the contents do not stain more deeply with eosin as do the contents of latex hyphae in *Arcangelicella*. The basidium with the differentiation of epibasidium is unusual in the present state of our knowledge, although suggestions of this kind of development are present in some of the Bornean species of *Arcangelicella*.

NORTH CAROLINA: Chapel Hill, Battle's Branch, J. N. Couch, type (Univ. N. Car. 7468, and Dodge).

20. *HYDNANGIUM HESSEI* (O. Kuntze) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 371. 1935.

*Octavianina Hessei* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Octaviania Hesseana* Saccardo & Sydow in Sacc. Syll. Fung. 14: 267. 1899.

*Octaviania mutabilis* Hesse, Hypog. Deutschl. 1: 77-78. 1891; Sacc. Syll. Fung. 11: 169. 1895—not *Octaviania mutabilis* Roumeguère, Rev. Myc. 7: 23. 1885.

Type: location not certainly known to us, but material so determined by Hesse collected in July, 1891, is in the Bot. Inst. Univ. Marburg.

Fructifications 1 cm. in diameter, white then yellowish-white, and finally dark brown flecked with yellowish-white, becoming greenish in light as in *A. asterosperma*, later dark brown or violet; peridium about 200  $\mu$  thick, easily separable in both fresh and dry material, fibrous to woolly, composed of hyaline, parallel hyphae of variable thickness next the gleba, hyphae thicker, more loosely woven and brown, thin-walled next the outside; gleba snow-white at first becoming dark brown, fragile at first becoming cartilaginous; cavities' long, irregular and filled with spores; septa composed of loosely woven, septate hyphae and slender subhymenial hyphae; basidia short, clavate, paraphyses shorter than the basidia, sterigmata filiform; spores very dark brown, 12-13  $\mu$  in diameter, coarsely echinate.

Germany. July and September.

GERMANY: Hessen-Nassau, *R. Hesse*, July 1891 (Hesse); Bayern, München, *F. Soehner* 961 (Soehner and Dodge).

21. *HYDNANGIUM LANIGERUM* (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

*Octaviania lanigera* Hesse, Hypog. Deutschl. 1: 79-80. 1891; Sacc. Syll. Fung. 11: 169. 1895.

*Octavianina lanigera* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898. Illustrations: Hesse, Hypog. Deutschl. 1: *pl.* 6, *f.* 7-8.

Type: location unknown to us, but authentic material in Farlow Herb. at Harvard Univ.

Fructifications 2.5  $\times$  2  $\times$  2 cm., reniform, pure white; fibrils snow-white, small, scanty; peridium 600-700  $\mu$  thick, loose, stupose to almost byssoid, composed of large, hyaline, septate hyphae 8-9.5  $\mu$  in diameter, sterile base broadly pulvinate;



gleba tawny to russet; septa 100–150  $\mu$  thick, composed of loosely woven, septate, branched hyphae 10  $\mu$  in diameter; basidia cylindric, 2–3-spored; spores spherical, 12–14  $\mu$  in diameter, tawny, with broad echinulae (10–14 per great circle) 2–3  $\mu$  long, walls 1–1.5  $\mu$  thick.

Under *Betula*. Germany. Early autumn.

GERMANY: Hessen-Nassau, Altmorschen, *B. Hesse* (Farlow).

22. *HYDNANGIUM JAVANICUM* P. Hennings, Beiblatt zur Hedwigia 40: (27). 1901; Saccardo & Sydow in Sacc. Syll. Fung. 16: 255. 1902; von Höhnelt, K. Akad. Wiss. Wien, math.-naturw. Kl. Sitzungsber. Abt. I. 117: 1017. 1908.

Type: in Bot. Mus. Berlin.

Fructifications subspherical, 1.8–2.1  $\times$  1.4–1.7 cm., drying 0.7–1.0 cm. in diameter, pale flesh-color, surface smooth or slightly tomentose; peridium about 140  $\mu$  thick, separable, of large, loosely woven hyphae 4  $\mu$  in diameter embedded in a gel; gleba flesh-color becoming brown, elastic, cavities minute, sinuous; septa about 40  $\mu$  thick, composed of slender, compactly woven, gelified hyphae; basidia clavate, 20–30  $\times$  5–8  $\mu$ , 4 sterigmata; spores spherical, densely echinate, brownish-olivaceous, 15–18  $\mu$  in diameter, with the spines yellowish, 3–4  $\times$  0.5–0.7  $\mu$ ; weak odor of rancid almonds.

JAVA: Tjibodas, *M. Fleischer*, 11 Oct. 1900, type (Berlin).

23. *HYDNANGIUM NIGRICANS* Kalchbrenner, Grevillea 10: 107. 1882; Saccardo, Syll. Fung. 11: 172. 1895.

Type: in Kew Herb. and in Bot. Mus. Berlin.

Fructifications 1.5  $\times$  2 cm., depressed-globose, drying black, smooth, no trace of sterile base or columella in sliced fructification; peridium 260–270  $\mu$  thick, composed of large, thin-walled prosenchyma; gleba ochraceous-tawny, cavities small; septa thin, 14–15  $\mu$  between hymenia (in dried material), appearing as slender, irregular, gelified hyphae but perhaps similar to the peridium, badly collapsed; basidia about 30  $\times$  11  $\mu$ , collapsing in the upper half on the separation of the spore; spores 12–19  $\mu$  in diameter, dark brown, with closely set, conical spines on a thick epispore.

Under *Acacia* in grassy fields. South Africa.

One should note that Kalchbrenner also cites *Macowan 1211* as *Macowanites agaricinus*.

SOUTH AFRICA: Somerset East, near Mt. Boschberg, *P. Macowan 1211*, type (Kew and Berlin).

24. *HYDNANGIUM TUBERCULATUM* (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 373. 1935.

*Octaviania tuberculata* Hesse, Hypog. Deutschl. 1: 75-77. 1891; Sacc. Syll. Fung. 11: 169. 1895.

*Octavianina tuberculata* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

Illustrations: Hesse, Hypog. Deutschl. 1: pl. 7, f. 14; pl. 9, f. 16-24.

Type: location unknown to us. Specimen examined from type locality collected two years after the type, determined by the author before the original description was published, but not cited.

Fructifications  $1.3 \times 2$  cm., depressed-globose, very irregular, deeply and thickly furrowed on the upper surface, white at first then yellowish, and finally brown vinaceous-buff to avellaneous in alcohol; sterile base disappearing at maturity; peridium 900-1000  $\mu$  thick, not separable, fibrous, composed of thin-walled, undulating, loosely woven, brownish hyphae 6-7  $\mu$  in diameter, becoming white next the gleba, woolly in the deep furrows; gleba mummy-brown, cavities very irregular, partially filled with spores; septa thin toward the outside, 90-100  $\mu$  thick, thicker between the cavities in the center of the fructifications, composed of large, thin-walled, septate hyphae 4-5  $\mu$  in diameter (almost pseudoparenchyma), white finally becoming light brown; basidia clavate with 3-4 sterigmata, filiform, half the length of the spores, paraphyses shorter, slenderer, and septate; spores with spiny, thick exospore, dark brown, 12-13  $\mu$  in diameter; odorless.

Under *Fagus sylvatica*. Hessen-Nassau, Germany. September and October.

GERMANY: Hessen-Nassau, Michelbach, *E. Hesse*, X/88 (Hesse).

25. *HYDNANGIUM DENSUM* Rodway, Papers & Proc. Roy. Soc. Tasmania 1919: 112. 1920; 1923: 160. 1924; Trotter in Sacc. Syll. Fung. 24: 1328. 1928.

*Hydnangium Mouchettii* herb. nom.

Type: in Rodway Herb. at Tasmanian Museum. Type of *H. Mouchettii* in Herb. Dept. Agr., Pathologist's Branch, Victoria.

Fructifications depressed-globose, 1–1.5 cm. in diameter when dry, pale ochre when fresh becoming cinnamon-buff to tawny-olive; peridium about 450  $\mu$  thick when dry, stupose, composed of thick-walled, brown hyphae 4–5  $\mu$  in diameter; gleba mummy-brown where cut, gray where fractured, resembling a *Melanogaster*, cavities filled with spores, polyhedral; septa very variable in thickness, composed of loosely woven, gelified, hyaline hyphae 2  $\mu$  in diameter, more compact in the subhymenium; basidia not seen; spores very dark brown, spherical, densely echinate, 10–11  $\mu$  in diameter.

The systematic position of this species is wholly obscure. Basidia if present are evanescent. From its spore-filled cavities it might be placed in *Melanogaster* or *Chondrogaster*, although its spore shape is closer to the dark-spored species of *Arcangeliiella*. It is even possible that it belongs in the Sclerodermataceae near *Pompholyx*.

AUSTRALIA: South Australia, Aldgate, [*Mouchette?*] (sub *Hydnangium Mouchettii* in Herb. Dept. Agr., Pathologist's Branch No. after 1444).

TASMANIA: Mt. Nelson Range, *L. Rodway*, type (Rodway).

26. *HYDNANGIUM LUTEUM* (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

*Octaviania lutea* Hesse, Jahrb. f. wiss. Bot. 16: 255. 1885; Hypog. Deutschl. 1: 74–75. 1891; DeToni in Sacc. Syll. Fung. 7: 491. 1888; Hollós, Magyar. Földalatti Gombai, 96, 207. 1911.

Illustrations: Hesse, Jahrb. f. wiss. Bot. 16: pl. 6, f. 7–9; Hypog. Deutschl. 1: pl. 6, f. 5–6; pl. 7, f. 49.

Type: in Upsala and Farlow Herbaria.

Fructifications up to 2.5–3 cm. in diameter, irregular to subglobose, becoming auburn, chestnut, or Mars brown in alcohol, surface smooth, fibrillose-villous, with lighter, almost white patches due to thicker portions of the peridium; peridium 300–400  $\mu$  thick in the thicker portions, 150–200  $\mu$  in the thinner, loosely stupose, composed of large, thin-walled, hyaline hyphae

as in *Rhizopogon maculatus*, fascicles of erect hyphae on the surface giving the villous appearance; sterile base not seen in older specimens, but evident in the younger; gleba cheesy in consistency, cinnamon to tawny-olive, cavities small, irregular, filled with spores; septa 40–50  $\mu$  thick, stupose, composed of parallel hyphae 3–4  $\mu$  in diameter; basidia 2–4-spored, clavate, 24–28  $\times$  12–13  $\mu$ ; spores 12–13  $\mu$  (15–16  $\mu$  with echinulae), tawny, with 12–18 spines on the periphery of an optical section of the spore.

Under birches. Germany. Summer.

GERMANY: Hessen-Nassau, Altmorschen, *E. Hesse*, type (Upsala and Farlow).

27. *HYDNANGIUM SOEHNERI* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 372. 1935.

Type: in Soehner, Zeller, and Dodge Herbaria.

Fructifications spherical to reniform, drying 0.6  $\times$  0.9 cm., very dark brown to black, no sterile base or columella seen; peridium 50–60  $\mu$  thick, of small-celled, gelified prosenchyma; gleba Sudan brown, cavities relatively large, empty; septa thin, somewhat scissile, of large, thick-walled, brownish, loosely woven hyphae; basidia large, cylindrical, soon collapsing; spores ellipsoidal, 15.4–18.2  $\times$  12.4–14  $\mu$ , dark brown.

GERMANY: Bayern, Wolfratshausen, Pupplinger Heide, *E. Soehner*, type (Soehner, Zeller, and Dodge).

28. *HYDNANGIUM CEREUM* Soehner, Kryptog. Forsch. 1: 394. 1924.

Type: in Soehner Herb. and portion in Dodge Herb.

Fructifications 2–3 cm. in diameter, spherical, smooth, glabrous, very firm, white then wax-yellow, often becoming tawny or Van Dyck brown in old age, drying tawny, base slightly rugose or depressed, no rhizomorphs; peridium thin, up to 100  $\mu$  thick; gleba white, later slightly yellowish, browning on exposure to air, tawny at maturity, drying ochraceous-buff, cavities small but conspicuous; spores spherical, hyaline at first, becoming slightly tawny, 10–15  $\mu$ , mostly 12.5  $\mu$ , in diameter, exospore slightly spinose when young, becoming coarsely echinate; odor slight when fresh, when dry, like that of apples.

In loam in oak forest. Ehrharting near Mühldorf. Very rare.

GERMANY: Bayern, Ehrharting bei Muhlendorf am Inn, *E Soehner 527*, type (Soehner and Dodge).

#### EXCLUDED SPECIES

1. *LEUCOPHLEBS Clelandi* (Rodway) Zeller & Dodge, comb. nov.

*Hydnangium Clelandi* Rodway, Papers & Proc. Roy. Soc. Tasmania 1924: 159. 1925.

Type: in Rodway Herb. at Tasmanian Museum.

Fructifications irregularly spherical, 1–2 cm. in diameter, whitish-ochre, drying light yellowish-olive to olive-yellow; peridium thin, membranous, white, continuous with the trama, outer 110  $\mu$  of large hyphae 7–8  $\mu$  in diameter, with gelified walls, inner 150  $\mu$  of slender, thin-walled hyphae 2–3  $\mu$  in diameter, densely interwoven; gleba dull brown-clay to umber, becoming browner with age, drying snuff-brown to bister, cavities about 1 mm., not contorted but densely crowded with spores; septa 14–15  $\mu$  thick, of densely woven, slender hyphae; spores pale yellow, globose, smooth, becoming obscurely verrucose, 20–22  $\mu$  in diameter, very thick-walled, somewhat suggesting *L. magnata* Harkn.

The type, consisting of a single fructification, does not seem to be in condition to show how the spores are borne, as all trace of hymenium has disappeared. In spore characters and general texture of the fructification it seems much closer to *Leucophlebs* than to *Hydnangium*.

TASMANIA: Hobart, Cascade Valley, *L. Rodway*, type (Rodway).

2. *HYDNANGIUM MICROSPORIUM* Rodway, Papers & Proc. Roy. Soc. Tasmania 1919: 111. 1920; 1923: 160. 1924; Trotter in Sacc. Syll. Fung. 24: 1328. 1928.—not *Octaviania microsporium* Mattiolo, nom. herb. in Lloyd Mus.

Type: in Rodway Herb. at Tasmanian Museum.

After a study of the type, we agree with Cunningham that this species should be referred to *Lycoperdon Gunnii* Berkeley.

## STEPHANOSPOREA

*Stephanospora* Patouillard, Bull. Soc. Myc. France 30: 349. 1914.

The type species of the genus is *Hydnangium caroticolor* Berkeley.

Fructifications spherical or nearly so, without sterile base or columella; peridium thin and fragile; gleba fragile; basidia cylindrical; spores long-ellipsoidal, coarsely echinate, with a broad collar at the base surrounding the sterigma.

It is with some hesitation that we have recognized this genus which is very close to *Hydnangium* in most characters, but its spore is so distinct and we have seen nothing which suggests a transition between it and *Hydnangium*. At present only a single species from England and central Europe is known.

STEPHANOSPOREA CAROTICOLOR (Berkeley) Patouillard, Bull. Soc. Myc. France 30: 349. 1914.

*Hydnangium caroticolor* Berkeley, Ann. & Mag. Nat. Hist. I. 13: 351-352. 1844; *Ibid.* I. 18: 76. 1846; Outlines British Fungol. 293. 1860; Tulasne, Fung. Hypog. 75. 1851; Winter in Rabenhorst, Krypt.-Fl. Deutschl. ed. 2. 1: 877-878. 1883; DeToni in Sacc. Syll. Fung. 7: 176-177. 1888; Masee, Ann. Bot. 4: 36-37. 1889 [often cited as Monogr. Brit. Gast.]; Hesse, Hypog. Deutschl. 1: 83-84. 1891; Patouillard, Bull. Soc. Myc. France 26: 203-204. 1910.

*Octaviania caroticolor* Corda, Icones Fung. 6: 36. 1854; Lloyd, Myc. Notes 67: 1141. 1922.

Illustrations: Berkeley, Outlines British Fungol. *pl.* 20, *f.* 1; Cooke, Handbook Brit. Fung. 1: 357; Corda, Icones Fung. 6: *pl.* 7, *f.* 65; Masee, Ann. Bot. 4: *pl.* 1, *f.* 6; Patouillard, Bull. Soc. Myc. France 25: 203, *f.* 3; Tulasne, Fung. Hypog. *pl.* 21, *f.* 4; Winter in Rabenhorst, Kryptog.-Fl. Deutschl. ed. 2. 1: 871.

Type: in Berkeley Herb. at Kew, and Broome Herb. at British Museum.

Fructifications oblong, about 2 cm. in diameter, slightly tomentose, pale orange-red [exactly like that of a fine carrot, Berkeley & Broome] when fresh, drying amber-brown to Argus

brown; peridium thin, fragile; gleba beautiful orange-red [Berkeley & Broome] when fresh, drying raw sienna, cavities small, empty; septa 10–14  $\mu$  thick, composed of parallel hyphae; basidia short-cylindric, sterigmata 3–4  $\mu$  long; spores long-ellipsoidal, with a smooth hyaline fold at the base, coarsely echinate, 8–13  $\times$  6–7  $\mu$ .

Central and western Europe.

GERMANY: Bayern, Kaufbeuren, *E. Soehner* 239 (Dodge, Zeller, and Berlin); Hessen-Nassau, Aue, *E. Hesse*, Aug. 1891 (Hesse).

FRANCE: Jura, Lepinay, *N. Patouillard*, Août, Oct. 1912 (Patouillard at Farlow).

SWITZERLAND: Bassecourt, *P. Konrad* (Lloyd Mus. 046); Zurich, *G. Winter* 1809 (Stanford and Berlin).

ENGLAND: *C. E. Broome* (Lloyd Mus. 0231.); Gloucestershire, near Clifton, *C. E. Broome*, type (Kew, Brit. Mus.); Leigh Wood, near Bristol, *C. E. Broome* 310 (ex Herb. J. W. Bailey in Brown Univ., Curtis Herb. at Farlow, and 4 collections Brit. Mus.); Dorsetshire, Swanage, Ballard Down, *C. E. Broome* (2 collections Brit. Mus., and Berlin).

# ELASMOMYCES, ARCANGELIELLA, AND MACOWANITES<sup>1</sup>

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*Elasmomyces* and *Arcangeliella* were erected by Cavara to receive those forms related to *Hydnangium* but having a columella. In *Elasmomyces* the gleba may pull away from the base of the substipitate columella at maturity, while in *Arcangeliella* the gleba remains attached to the columella although the peridium may break away from the base partially exposing the lower part of the gleba. *Arcangeliella* also has lactiferous ducts in the trama, the peridium, and the columella. These characters seem important from the standpoint of comparative morphology and are worthy of generic distinction. The lactiferous ducts at times are scant and may require careful staining. The study of the columella in fresh material is rather simple, but in dry herbarium specimens it may not show more than as a line. If whole or large sections of specimens are present they may be made to regain almost natural stature by soaking, rendering even a slight columella apparent and readily studied. When the fructifications have been sliced thin, as in many of the older collections, this character may be ambiguous.

*Macowanites* is similar to the above two genera in some respects, but for the most part the species are larger and are more pileate than in *Elasmomyces*. One species with lactifer-

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ous ducts in the fundamental tissues may be most closely allied to *Arcangelhiella*.

We have used the same color standards (Ridgeway) and in citing specimens studied have used the same abbreviations as in our other recent papers. Besides those whose aid was gratefully acknowledged in previous papers we are indebted for financial aid to the American Association for the Advancement of Science (grant in 1923 to the senior author), to the John Simon Guggenheim Memorial Foundation which appointed the junior author a fellow to Europe in 1930, and to the Science Research Fund of Washington University for a grant in 1933 to the junior author.

#### ELASMOMYCES

*Elasmomyces* F. Cavara, *Malpighia* 11: 414-428. 1897; *Rev. Myc.* 21: 23. 1899; Saccardo & Sydow in *Sacc. Syll. Fung.* 14: 258. 1899; Petri, *Fl. Ital. Cryptog.* 1<sup>5</sup>: 29. 1909; Hollós, *Magyar. Földalatti Gombai*, 81-82, 201. 1911.

*Secotium* sect. *Elasmomyces* E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam.* I. 1<sup>\*7</sup>: 300. 1900.

The type species of the genus is *Elasmomyces Mattirolanus* F. Cavara.

Fructifications subspherical when young, sometimes expanding like a small agaric button, but the gleba only slightly separating from the stipe, which is usually short and slender; peridium covering the gleba but pulling away around the base of the stipe, exposing the gleba below and sometimes flaking off irregularly on other parts of the fructification; gleba of anastomosing cavities; spores spherical, echinulate.

1. *ELASMOMYCES BORNEENSIS* (Petri) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 370. 1935.

*Octaviania borneensis* Petri, *Malpighia* 14: 128. 1900; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 248. 1902.

Illustrations: Petri, *Malpighia* 14: *pl.* 2, *f.* 12, 19, 20; *pl.* 3, *f.* 4.

Type: in *Ist. Bot. Univ. Firenze*.

Fructifications spherical to slightly elongate, attenuated below; surface dirty white, felt-like, covered with patches where

the peridium is thicker; columella penetrating beyond the center of the fructification; sterile base present; peridium about 1 mm. thick, not separable, similar in texture to the gleba, the outside hyphae larger, forming a loosely woven layer, irregular in thickness; gleba very dark, cavities very small; septa thick in comparison with the cavities, trama of hyphae irregularly traversing a gelatinous stratum; basidia cylindrical, 4-, rarely 2-spored, sterigmata short; spores spherical, yellow-greenish, 9–10  $\mu$  in diameter, spines similar to those of *Arcangelietta asterosperma*.

Sarawak, Borneo.

The presence of the columella and the hyphae being embedded in a gelatinous layer in the septa seem to indicate that this species may belong in *Arcangelietta*, near *A. vulvaria*, although no lactiferous ducts were found.

BORNEO: Sarawak, O. Beccari 1867, type (Univ. Firenze).

2. *ELASMOMYCES ECHINOSPORUS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 370. 1935.

*Macowanites echinosporus* Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 57–58. 1919.

Type: in Univ. Cal., Dodge, and Zeller Herbaria.

Fructifications subspherical to irregular, 1  $\times$  1.5 cm., even, smooth, very delicate salmon-color, becoming tawny-olive in alcohol; peridium thin, 90–120  $\mu$  thick, extending over the upper half of the fructification, consisting of hyaline pseudoparenchyma; stipe concolorous, about 5 mm. long and 2 mm. in diameter, stipose, of fine, hyaline hyphae; sterile base a conical projection of the stipe extending into the gleba but not percurrent; gleba covered above, exposed below, sinuate about the stipe, concolorous with the peridium, cavities minute, irregular; septa 60–80  $\mu$  thick (including hymenia), hyaline, composed of pseudoparenchymatous cells, not scissile; cystidia rare, clavate, apiculate, 9–10  $\times$  20–24  $\mu$ , hyaline; basidia small, cylindrical to clavate, 2–4-spored, 5–8  $\times$  18–22  $\mu$ ; spores spherical to broadly ovoid, hyaline, appendiculate, 6–8  $\mu$  in diameter, sparingly echinulate.

Hypogeous under *Quercus*. California. March.

CALIFORNIA: Alameda County, East Oakland, *N. L. Gardner 402*, type (Univ. Cal., Dodge, and Zeller 1624).

3. *ELASMOMYCES MATTIROLANUS* F. Cavara, *Malpighia* 11: 426. 1897; *Rev. Myc.* 21: 23-24. 1899; Saccardo & Sydow in *Sacc. Syll. Fung.* 14: 258. 1899; Petri, *Fl. Ital. Cryptog.* 1<sup>5</sup>: 30-31. 1909; Hollós, *Magyar. Földalatti Gombai*, 81-82. 201. 1911.

*Secotium (Elasmomyces) Mattirolanum* E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam.* I. 1<sup>\*\*</sup>: 301-302. 1900.

Illustrations: F. Cavara, *Malpighia* 11: *pl.* 7; *Rev. Myc.* 21: *pl.* 187, *f.* 1-5; E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam.* I. 1<sup>\*\*</sup>: 301-302. *f.* 150 *A-F*; Petri, *Fl. Ital. Cryptog.* 1<sup>5</sup>: *f.* 6-7.

Type: in R. Ist. Bot. di Napoli, Mattirola Herb., a portion in Dodge and Zeller Herbaria.

Fructifications 1.5-2.5 cm. in diameter, depressed-globose, resembling the young buttons of *Agaricus*, margin undulate, yellowish-white, pruinose; stipe short, thick, continued as a thick percurrent columella through the gleba, filamentous with islands of pseudoparenchyma; peridium 210-220  $\mu$  thick, outer hyphae slender and periclinal, gradually becoming larger and more prosenchymatous within; gleba drying tawny-olive to wood-brown, cavities large, empty; septa 110-120  $\mu$  thick, composed of slender, periclinal, loosely woven hyphae; basidia cylindric, 2-spored; spores slightly ellipsoidal, dilute straw-yellow, about  $10 \times 7 \mu$ , with slender spines.

Emergent under conifers. Italy and Oregon. (May in Oregon.)

ITALY: Vallombrosa, *F. Cavara*, type (R. Ist. Bot. di Napoli, Mattirola Herb., Dodge, and Zeller); Firenze, *O. Mattirola* (Patouillard Herb. at Farlow).

OREGON: Lincoln County, Waldport, *S. M. Zeller 7113* (Dodge and Zeller).

#### ARCANGELIELLA

*Arcangelietta* F. Cavara, *Nuov. Giorn. Bot. Ital. N. S.* 7: 117-128. 1900; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 255-256. 1902; Lloyd, *Myc. Notes* 7: 1142. 1922.

*Octaviania* Vittadini, *Monogr. Tuberac.* 15-20. 1831 (pro parte minore).

*Octaviania* Vittadini em. Corda, Anleit. z. Stud. Myc. 107, lxxxii. 1842; Icones Fung. 5: 26. 1842; Tulasne, Ann. Sci. Nat. Bot. II. 19: 376. 1843; Fung. Hypog. 77. 1851; Fries, Summa Veg. Scand. 436. 1849; Berkeley, Outlines Brit. Fungol. 292. 1860; Winter in Rabenhorst, Krypt.-Fl. Deutschl. ed. 2. 1: 878. 1884; De Toni in Sacc. Syll. Fung. 7: 158-161. 1888; Hesse, Hypog. Deutschl. 1: 71-81. 1891; E. Fischer in Engler & Prantl, Die Nat. Pflanzenfam. I. 1<sup>\*\*</sup>: 310. 1899, and ed. 2, 7a: 17. 1933; Hollós, Magyar. Földalatti Gombai, 95-96, 206-207. 1911; Lloyd, Myc. Notes 7: 1139-1142. 1922 (pro parte).

*Octavianina* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898 (pro parte).

*Octaviana* Rodway, Papers & Proc. Roy. Soc. Tasmania 1923: 157. 1924.

*Gymnomyces* Masee & Rodway, Kew Bull. Misc. Inf. 1898: 125. 1898; Saccardo & Sydow in Sacc. Syll. Fung. 16: 249. 1898; E. Fischer in Engler & Prantl, Die Nat. Pflanzenfam. I. 1<sup>\*\*</sup>: 557. 1900, and ed. 2, 7a: 14. 1933; Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 54-56. 1919.

The type species of the genus is *Arcangeliella Borziana* F. Cavara. In 1831 Vittadini described seven species of *Octaviania* without designating the type. Six of these species have been universally referred by writers since to *Melanogaster* Corda, published the same year. Some of the type specimens have been lost and some of the species have not been collected and identified with Vittadini's species since. However, *O. variegata* Vitt. has had a continuous tradition and is well known, being the commonest in Italy, and may be considered the type of *Octaviania*.

Corda in 1842, and Tulasne the next year, attempted to transfer the name *Octaviania* to another group of hypogeous Gasteromycetes by selecting *O. asterosperma* (referred by us to *Arcangeliella*) as the type. A careful reading of Vittadini's descriptions and discussions shows that the principal character which he emphasized was the dark color of the spores, the same as Corda for *Melanogaster*, and that the shape of the spore and the distribution of basidia in the gleba were quite secondary characters to Vittadini. He specifically notes that *O. astero-*

*sperma* is aberrant in the genus because of its sterile base and the shape of its spores, the two characters used by Corda and Tulasne in their later work. Consequently we prefer to regard *Octaviania* as a synonym of *Melanogaster*. O. Kuntze in 1898 recognized this situation and proposed *Octavianina*, treating four species here placed in *Hydnangium* and four which we have treated as *Arcangeliella*. He failed to designate a type and apparently did not study specimens, basing his concept wholly on that of DeToni in Sacc. Syll. Fung. 7: 158-160. 1888. Any attempt to select a type must be arbitrary. One might choose *Octaviania asterosperma* and place all the species here treated as *Arcangeliella* in *Octavianina*, while if another species were chosen as the type species *Octavianina* would become a synonym of *Hydnangium*, which Kuntze also recognized as a separate genus. We prefer to overlook this name as a source of confusion. It has not been used to our knowledge since proposed by Kuntze.

*Octaviana* Rodway is evidently only an error in orthography and should not be given separate recognition.

*Gymnomycetes* Masee & Rodway was based on *G. pallidus* and *G. seminudus* without designation of type. Clements & Shear, Gen. Fung. 356. 1931, selected *G. pallidus* as the type but gave no reasons for their choice. Since this species is described as having "no distinct peridium," while *G. seminudus* has a "delicate external downiness which may be considered as a very rudimentary peridium," and since the principal character in Masee & Rodway's generic description is "Peridium haud distinctum vel nullum," their choice is reasonable. Both species are here treated in *Arcangeliella*, most of whose species have a well-developed peridium even though at maturity it may be evanescent or easily dehiscent from the base or lower half of the fructification in several species. To recognize *Gymnomycetes* for this group is also undesirable as it has been used for various groups of species and none of the essential characters has been ascribed to it. To adopt it would also be confusing. *Arcangeliella* was very carefully described with all the essential characters of the group and has had a continuous tradition since as additional species have been described. Therefore

we propose to recognize it (although arguments from a strict interpretation of the International Rules of Botanical Nomenclature might be brought for *Octavianina*) and recommend *Arcangelietta* to the next botanical congress as a *nomen conservandum*.

Fructifications gregarious, hypogeous or emergent, fleshy, lactiferous; peridium thin, especially below, where it reaches the base in young specimens but where it is often evanescent at maturity; columella usually percurrent, sometimes branched; base more or less sterile, usually attenuated into a stipe-like attachment to the rhizomorphs, generally lactiferous; gleba fragile or cheesy, lactiferous, cavities variable in size, often minute, irregular, radiating more or less from the columella and base; basidia 2–4-spored; cystidia sometimes present; spores spherical to ellipsoidal, echinulate to verrucose, often alveolate or somewhat reticulate.

#### KEY TO SPECIES OF ARCANGELIELLA

1. Spores smooth or very slightly wrinkled above, subspherical, 4–6  $\mu$  in diameter.....1. *A. glabrella* (p. 608)
1. Spores echinulate, verrucose, reticulate or alveolate..... 2
  2. Spores definitely obovoid; fructifications viscid..... 3
  2. Spores ellipsoid or ovoid..... 4
  2. Spores spherical..... 13
3. Fructifications violet; spores finely asperate except the coarse verrucose surface of the distal end, 7.5–9.6 (–10)  $\times$  5.5–7.4  $\mu$ .....2. *A. violacea* (p. 608)
3. Fructifications tawny; spores smooth to slightly asperate or verrucose, especially on the upper half, 11–15  $\times$  7.4–8.2  $\mu$ .....3. *A. nana* (p. 609)
  4. Spores with a wrinkled utricle, or alveolate or reticulate..... 5
  4. Spores merely rugose, verrucose, or echinulate..... 8
5. Spores alveolate, ellipsoid, dark brown, 10–12  $\times$  6–7.4  $\mu$ .....
  - .....4. *A. ellipsoidea* (p. 610)
5. Spores citriform, with the utricle inconspicuously wrinkled longitudinally, 11–15  $\times$  8–11  $\mu$ ; peridium 1.5 mm. thick.....5. *A. ambigua* (p. 610)
5. Spores reticulate or reticulate-echinulate..... 6
  6. Spores averaging more than 11  $\mu$  long, reticulate-echinulate, broadly ellipsoid, 10–13  $\times$  6–11  $\mu$ .....6. *A. Gardneri* (p. 611)
  6. Spores averaging less than 11  $\mu$  long, reticulate..... 7
7. Peridium whitish, of fine hyphae, 100–300  $\mu$  thick; spores hyaline, broadly ellipsoid, arcuate-reticulate, 8–11  $\times$  7.4–9  $\mu$ .....7. *A. Curtisii* (p. 612)
7. Peridium violet, of gelified hyphae, 100–115  $\mu$  thick; spores light brown, ellipsoid, obtusely pointed, pedicellate, shallowly and finely areolate-reticulate, 8–10 (–11)  $\times$  4.4–5.6 (–7)  $\mu$ .....8. *A. Campbellae* (p. 613)

9. Peridium more than 1 mm. thick; spores citriform, with slightly wrinkled  
utricle,  $11-15 \times 8-11 \mu$ .....5. *A. ambigua* (p. 610)
8. Spores more than  $12 \mu$  long..... 9
8. Spores less than  $12 \mu$  long..... 12
9. Peridium less than 0.6 mm. thick; spores broadly ellipsoid with round ends 10
10. Spores hyaline, echinulate,  $14.5-15.5 \times 11-12 \mu$ .....9. *A. Stephensii* (p. 613)
10. Spores hyaline, reticulate-echinulate,  $10-13 \times 6-11 \mu$ .....  
.....6. *A. Gardneri* (p. 611)
10. Spores brown, verrucose,  $11-20 \times 8-13 \mu$ ..... 11
11. Peridium duplex, both layers of periclinal hyphae.....10. *A. africana* (p. 614)
11. Surface of peridium of periclinal hyphae.....11. *A. Behrii* (p. 615)
11. Surface of peridium of erect septate hyphae.....  
.....11a. *A. Behrii* var. *caudata* (p. 616)
11. Peridium duplex, outer layer prosenchymatous,  $110-115 \mu$  thick, inner  
layers of slender periclinal hyphae.....12. *A. seminuda* (p. 617)
12. Spores alveolate, ellipsoid, dark brown,  $10-12 \times 6-7.4 \mu$ ; peridium  
 $170-350 \mu$  thick.....4. *A. ellipsoidea* (p. 610)
12. Spores verrucose, especially at distal end, ellipsoid, rounded above,  
brown,  $7.5-9.6 (-10) \times 5.5-7.4 \mu$ ; peridium  $60-100 \mu$  thick.....  
.....2. *A. violacea* (p. 608)
12. Spores completely verrucose, thick-walled, brown,  $9.5-12.5 \mu$  long;  
peridium  $150-500 \mu$  thick.....*Hydnangium purpureum* (p. 589)
12. Spores reticulate, broadly ellipsoid to subspherical, hyaline,  $8-11 \times$   
 $7.4-9 \mu$ ; peridium  $100-300 \mu$  thick.....7. *Arcangeliiella Curtisi* (p. 612)
12. Spores reticulate-echinulate, broadly ellipsoid to subspherical, hyaline,  
 $10-13 \times 6-11 \mu$ ; peridium  $100-150 \mu$  thick.....6. *A. Gardneri* (p. 611)
13. Spores alveolate..... 14
13. Spores echinulate..... 16
13. Spores reticulate..... 27
14. Surface of peridium with layer of erect hyphae, giving plushiness to  
surface; spores minutely alveolate-echinulate,  $10-12 \mu$  in diameter,  
yellowish.....13. *A. pilosa* (p. 619)
14. Surface without erect hyphae..... 15
15. Spores hyaline, alveolate-reticulate,  $11-12.5 \mu$  in diameter (giants  $12.5-15.5$   
 $\mu$ ); peridium of gelified interwoven hyphae.....15. *A. Ravennii* (p. 622)
15. Spores yellow, alveolate-echinulate,  $9-11 \mu$  in diameter; peridium pros-  
enchymatous.....22. *A. crenea* (p. 628)
15. Spores brown, alveolate, and ragged,  $12-15 \times 11-13 \mu$ ; peridium duplex,  
outer part of prosenchyma and inner of loosely interwoven hyphae.....  
.....12. *A. seminuda* (p. 617)
15. Spores very light yellowish, echinulate-reticulate,  $8-15 \mu$  in diameter,  
(giants  $16-19 \mu$ ); peridium of polyhedral-celled parenchyma covered by a  
fibrous layer of periclinal hyphae; gleba pinkish.....16. *A. socialis* (p. 623)
15. Spores dark yellowish, very finely and deeply alveolate-echinulate,  $11-15 \mu$   
in diameter; peridium of parenchyma with outer layer of compact pros-  
enchyma; gleba cream-color.....17. *A. scissilis* (p. 624)
16. Surface of the peridium with erect hyphae; spores  $10-12 \mu$  in diameter  
.....13. *A. pilosa* (p. 619)
16. Surface without erect hyphae..... 17

17. Spores showing ridges or reticulations on the surface..... 18
17. Spores strictly echinulate (except short ridges in *A. vulvaria*)..... 21
  18. Spores less than 12  $\mu$  in diameter..... 19
  18. Spores more than 12  $\mu$  in diameter..... 20
19. Peridium 100–300  $\mu$  thick; spores 8–11  $\times$  7.4–9  $\mu$ .....7. *A. Curtisii* (p. 612)
19. Peridium 55–80  $\mu$  thick; spores 7–9 (–11)  $\mu$  in diameter.....
  - .....14. *A. alveolata* (p. 620)
  20. Spores hyaline, reticulate alveolate.....15. *A. Ravenelii* (p. 622)
  20. Spores brown, alveolate.....12. *A. semmuda* (p. 617)
21. Spores averaging less than 11 $\mu$  in diameter..... 22
21. Spores averaging more than 11  $\mu$  in diameter..... 23
  22. Spores dark brown, 9–14.5  $\mu$  in diameter, with conical echinulae..... 23
    - .....18. *A. tasmanica* (p. 624)
  22. Spores hyaline, 7–18  $\mu$  in diameter, with acicular echinulae.....
    - .....19. *A. australiensis* (p. 625)
  22. Spores citrine-yellow, sparsely short-echinulate, 8–11.5  $\mu$  in diameter..
    - .....30. *A. krjukowensis* (p. 626)
  22. Spores hyaline or light yellowish, with acicular echinulae, 8–11  $\mu$  (–13  $\mu$ ) in diameter.....21. *A. borziana* (p. 628)
  22. Spores yellow, alveolate, having about 24 spines per great circle, 9–11  $\mu$  in diameter.....22. *A. crema* (p. 628)
23. Spores echinulate but also with short ridges, 9–12  $\mu$  in diameter.....
  - .....23. *A. vulvaria* (p. 629)
23. Spores echinulate..... 24
  24. Echinulae acicular..... 25
  24. Echinulae coarse and conical..... 26
25. Peridium of slender gelified interwoven hyphae; spores 11–12  $\mu$  in diameter, spherical.....24. *A. occidentalis* (p. 629)
25. Peridium of compact interwoven hyphae; spores 14.5–15.5  $\times$  11–12  $\mu$ ....
  - .....9. *A. Stephensii* (p. 613)
25. Peridium pseudoparenchymatous with rind of prosenchyma; spores 11–15  $\mu$  in diameter; gleba creamy.....17. *A. scissilis* (p. 624)
25. Peridium of polyhedral-celled parenchyma; spores 8–15 (–19  $\mu$ ) in diameter; gleba pink.....16. *A. socialis* (p. 623)
  26. Spores hyaline or light yellowish, 11–17  $\mu$  in diameter, epispore thick; fructification pale rose.....25. *A. rosea* (p. 630)
  26. Spores dark brown, 13–16  $\mu$  in diameter, epispore not easily seen, spines large, 2  $\mu$  long; fructification white with rufescent tints, darkening.....26. *A. asterosperma* (p. 631)
  26. Spores brown, 9–14.5  $\mu$  in diameter, epispore thick; fructifications brownish, drying black.....18. *A. tasmanica* (p. 624)
27. Spores with discontinuous ridges, 11–15  $\mu$  in diameter; peridium about 640  $\mu$  thick.....27. *A. Beccari* (p. 635)
27. Spores with discontinuous ridges but also echinulate, 9–12  $\mu$  in diameter; peridium 1200–1440  $\mu$  thick.....28. *A. vulvaria* (p. 629)
27. Spores with a few irregular ridges and sometimes slightly echinulate, 7–9 (–11)  $\mu$  in diameter.....14. *A. alveolata* (p. 620)
27. Spores alveolate-reticulate (reticulations regular), 11–12.5 (–15.5)  $\mu$  in diameter.....15. *A. Ravenelii* (p. 622)



27. Spores roughly and irregularly areolate-reticulate,  $8-11 \times 7.4-9 \mu$  in diameter.....7. *A. Curtisii* (p. 612)

1. *ARCANGELIELLA GLABRELLA* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 368. 1935.

Type: in Lloyd Mus., Dodge, and Zeller Herbaria.

Fructifications 1-1.5 cm. in diameter (drying 0.5-1.0 cm.), subglobose to depressed-globose, smooth, white to brownish, drying sordid white to buckthorn-brown; columella percurrent, of fibrillose tissue with lactiferous ducts and islands of hyaline, soft parenchyma; peridium about  $640 \mu$  thick above to  $80-130 \mu$  thick on the sides and below, of large-celled parenchyma with a surface or rind layer of compact, interwoven hyphae with lactiferous ducts; gleba white, drying ivory-yellow to cream-buff, cavities nearly spherical; septa thin, extremely scissile, of parallel hyphae with lactiferous ducts; in young specimens cylindrical cystidia (?), the dilated terminals of lactiferous ducts, breaking and exuding globules of latex; spores hyaline, smooth to slightly wrinkled above, pedicellate, subspherical,  $4-6 \mu$  in diameter.

Australia and Tasmania. June to July.

The cystidia in this species are similar in size and shape to those reported by Setchell in *Arcangeliella alveolata* (*Elasmo-mycetes russuloides*).

AUSTRALIA: Victoria, Lilydale, *F. Campbell* 27b (Broome Herb. at Brit. Mus.); *F. (Campbell) Martin* 467 (Kew).

TASMANIA: Kingston, Leslie Road, *L. Rodway* 1111 as *Gymnomyces pallidus*, type (Lloyd Mus., Dodge, and Zeller).

2. *ARCANGELIELLA VIOLACEA* (Massee & Rodway) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 369. 1935.

*Hymenogaster violaceus* Massee & Rodway, Kew Bull. Misc. Inf. 1898: 127. 1898; Saccardo & Sydow in Sacc. Syll. Fung. 16: 253. 1902; Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 29. 1912.

Type: in Kew Herb.

Fructifications spherical to irregular, 2-3 cm. in diameter; surface smooth, viscid, lilac-fuscous then violet, drying orange-cinnamon, Mikado brown, or Saccardo's umber; sterile base small but distinct, with a usually percurrent columella,

with pseudoparenchymatous tissue; peridium 60–100  $\mu$  thick, composed of gelified pseudoparenchyma without and interwoven hyphae with lactiferous ducts within; gleba white then brown, drying Sayal brown; septa 36–45  $\mu$  thick, composed of hyaline hyphae with lactiferous ducts; basidia 11–16  $\times$  4  $\mu$ , cylindrical to clavate, sterigmata variable in length; spores obovoid, usually pedicellate, asperate with coarse warts above, 7.5–9.6 (–10)  $\times$  5.5–7.4  $\mu$ .

Tasmania.

TASMANIA: Proctors Road, *L. Rodway 1262* (Dodge and Zeller); Cascades, Hobart, *L. Rodway 1106* (Lloyd Mus. 075, and Dodge); *L. Rodway 297*, type (Kew).

3. *ARCANGELIELLA NANA* (Masse & Rodway) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 368. 1935.

*Hymenogaster nanus* Masse & Rodway, Kew Bull. Misc. Inf. 1899: 180. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 256. 1902; Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 29. 1912; 1923: 153. 1924.

Type: in Kew Herb.

Fructifications 1.3 cm. high and broad, pyriform with a prominent sterile base, surface tawny-brown drying avellaneous to army-brown, smooth, viscid when moist; sterile base well developed, of prosenchyma with lactiferous ducts; peridium duplex, outer layer 180–200  $\mu$  thick, clear hyaline, of very gelified hyphae, inner layer 100–150  $\mu$  thick, dark brown, of collapsed stupose tissue, with large lactiferous ducts; gleba dark tawny-brown, drying russet-vinaceous, with a pallid yellowish, percurrent columella which dries pinkish-cinnamon; septa hyaline to brownish, of a loose prosenchyma, with a few lactiferous ducts, 35–40  $\mu$  thick; basidia 2–4-spored, 14–20  $\times$  6  $\mu$ ; spores narrowly obovoid, dark brown, smooth to slightly asperate, especially on the upper half, 11–15  $\times$  7.4–8.2  $\mu$ .

Tasmania and South Australia. August.

*Rodway 1272* has much broader spores than the type of *A. nana* but seems identical in other characters.

TASMANIA: Hobart, *L. Rodway 609*, type (Kew and Lloyd Mus.); *L. Rodway 1272* (Dodge and Zeller).

AUSTRALIA: S. Australia, Encounter Bay, *J. B. Cleland 5* (Dodge).

4. *ARCANGELIELLA ELLIPSOIDEA* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935.

Type: in Dodge and Zeller Herbaria.

Fructifications drying 0.7–3.0 cm. broad and 1–2 cm. high, depressed-subglobose, pyriform to reniform in vertical section, smooth, drying honey-yellow to isabella-color; sterile base prominent in young specimens, extended above into a percurrent (or nearly so) columella; peridium 170–350  $\mu$  thick, composed of a hyaline prosenchyma of large cells pierced by periclinal strands of hyphae including lactiferous ducts; gleba drying cinnamon-rufous to hazel, cavities relatively large; septa 30–65  $\mu$  thick, of fibrous prosenchyma, easily scissile; spores ovoid when young, ellipsoid at maturity, dark brown, finely alveolate, 10–12  $\times$  6–7.4  $\mu$ .

Since this collection was originally identified by Rodway as *Hymenogaster violaceus* (*Arcangeliella*) its colors when fresh doubtless are similar to that species.

TASMANIA: Hobart, L. Rodway 1236, as *Hymenogaster violaceus*, type (Dodge and Zeller).

5. *ARCANGELIELLA AMBIGUA* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 365. 1935.

Type: in Univ. Cal., Dodge, and Zeller Herbaria.

Fructifications pyriform to irregularly and variously lobed, up to 5 cm. broad and 3 cm. high, dirty white turning blue when touched, then wine-colored or black, drying honey-yellow to light brownish-olive, surface smooth to rimose and flaky due to splitting of a very thick peridium; sterile base prominent, stipitiform in some plants, drying corky, as well as other localized islands of sterile tissue; columella prominent and percurrent; peridium very thick, drying 1.5 mm. thick above, flaking off in patches and sometimes exposing the gleba below, composed of large, closely woven hyphae (4–7.5  $\mu$  in diameter) penetrated by numerous lactiferous ducts, and periclinal strands of prosenchyma of smaller hyphae which become the predominant type of tissue next to the gleba; gleba chocolate-color to wine-color when fresh, developing from the base upward, cavities small, sinuous, young parts just under the upper

peridium antique brown to auburn, older parts dry, blackish-brown; septa fragile, disintegrating in older specimens, of large, compactly interwoven hyphae penetrated by scattered lactiferous ducts,  $35\text{--}45\ \mu$  thick; basidia  $20\text{--}24 \times 6\text{--}8\ \mu$ , clavate, 2- or 4-spored, sterigmata short, about  $6\text{--}8\ \mu$  long,  $1\text{--}2\ \mu$  in diameter; spores dark brown, ovoid to ovoid-citriform, sometimes with a broad apiculus, usually attenuated below to the breadth of the sterigma, with inconspicuous utricle, with 9–10 faintly visible longitudinal ribs; young spores  $13\text{--}15 \times 8\text{--}9\ \mu$ , mature spores  $11\text{--}15 \times 8\text{--}11\ \mu$ ; odor of old leather.

Cespitose; partly immersed in hard soil under oak. California. May and June.

This large wine-colored species seems to be a transitional complex, partaking of the characters of various genera. Because of its sterile base, percurrent columella, and lactiferous ducts in all the sterile and tramal tissues, the species has been placed in *Arcangeliiella*. In sterile tissues it seems to have close affinities within the genus to *A. Beccari* and *A. vulvaria*, as well as *Phallobata* and *Phallogaster*, but the spores are somewhat similar in shape to those of certain species of *Hymenogaster* and their ribbed surface somewhat like that in *Gautieria*.

CALIFORNIA: Santa Clara County, Saratoga, Dale Parks, type (Univ. Cal. as H. E. Parks 825, Z 31, also Dodge and Zeller 1810, 7820).

6. *ARCANGELIELLA GARDNERI* (Zeller & Dodge) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935.

*Gymnomyces Gardneri* Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 54–55. 1919.

Type: in Univ. Cal., Zeller, and Dodge Herbaria.

Fructifications subglobose to irregular, depressed,  $2.5 \times 1.5 \times 1.5$  cm. in alcohol, drying  $1.4 \times 0.8 \times 0.8$  cm., cream-color to yellow-ochre in alcohol, drying tawny-olive; peridium  $100\text{--}150\ \mu$  thick, of homogeneous hyaline prosenchyma, except a narrow scissile layer of periclinal hyphae next to the gleba; columella dendroid, resembling much-thickened septa, of quite gelified, hyaline hyphae, with lactiferous ducts, drying russet-brown; gleba drying cream-color to clay-color, cavities small, globose

to irregular; septa hyaline, 60–80  $\mu$  broad, with lactiferous ducts; basidia hyaline, clavate 2-spored, 25–29  $\times$  9–10  $\mu$ , sterigmata slender, 6–7  $\mu$  long; spores subspherical, usually somewhat elongate, hyaline *sub lente*, 6–11  $\times$  10–13  $\mu$ , reticulate, rugose under oil immersion; latex white (Parks).

Under leaves of *Quercus agrifolia*. Pacific coast. December.

The locality in Texas must remain doubtful unless confirmed by further specimens, as the late C. G. Lloyd was sometimes careless in preserving original labels. George L. Fisher sometimes used a printed label with his address and may not have changed it to conform with each collection. Lloyd often recorded the address of a correspondent instead of the locality of collection.

?TEXAS: Harris County, Houston, *Geo. L. Fisher* (Lloyd Mus. 65).

OREGON: Benton County, Corvallis, *L. M. Booser* 41 (Oregon State 3393, and Zeller 2208); *H. P. Barss* (Zeller 1728)

CALIFORNIA: no locality, *H. E. Parks* (Zeller); *Parks* 1130 (Dodge); Alameda County, Berkeley, *N. L. Gardner*, type (Univ. Cal. 376, Zeller 1618, and Dodge); Santa Clara County, *H. E. Parks* 913, Call of the Wild, *H. E. Parks* 913 A, Alder-croft, *H. E. Parks* 64, *H. E. Parks & C. W. Dodge* 1528, Guadalupe Mines, *H. E. Parks* 211, 2348, 2429, 5 (1917), 273, 943b, and 3/4/21, *H. E. Parks & Dale Parks* 943, Saratoga, *H. E. Parks* 996 (all Univ. Cal., Dodge, and Zeller).

7. *ARCANGELIELLA CURTISII* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935.

*Hydnangium Ravenelii* Farlow in Foerste, Bot. Gaz. 19: 37. 1894.—*non aliorum*.

Type: in Mo. Bot. Gard., and Curtis Herb. at Farlow.

Fructifications drying 0.7–1.4 cm. in diameter and isabella-color to brownish-olive; peridium 100–300  $\mu$  thick, soft, fibrillose, of very fine periclinal hyphae, with lactiferous ducts forming the core of quite definite hyphal strands; gleba drying pinkish-buff to cinnamon-buff; septa drying 30–40  $\mu$  thick, stupose, scissile; spores subspherical to broadly ellipsoidal, 8–11  $\times$  7.4–9  $\mu$ , roughly areolate-reticulate.

This species differs from *A. Ravenelii* and *A. Gardneri* in spore size, surface characters, and structure of the peridium.

SOUTH CAROLINA: Darlington County, Society Hill, *M. A. Curtis*, type (Mo. Bot. Gard. 5647, and Farlow).

GEORGIA: Bainbridge, *E. Foerste* (Farlow).

8. *ARCANGELIELLA CAMPBELLAE* Berkeley & Broome in Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Hymenogaster Campbellii* Berkeley & Broome, herb. nom.

Type: in N. Y. Bot. Gard. Herb., Lloyd Mus., and Kew Herb.

Fructifications subspherical, obovoid to much lobed, attenuated below, 1–2.5 cm. in diameter, cespitose, “violet color outside” [Miss Campbell], drying clay-color to tawny-olive, surface dull, even, glabrous; sterile base prominent, attenuate stalk-like below, extending as a cone into the gleba or as a percurrent or branched columella, white within, of a very spongy, open-meshed prosenchyma of hyaline hyphae; peridium 100–115  $\mu$  thick, of very even thickness, composed of gelified, hyaline, interwoven hyphae with lactiferous ducts, periclinal on the surface, diagonal in the outer third, loosely periclinal in the middle third, more slender and closely periclinal in the inner third; gleba ochraceous-tawny (dry), cavities radiating from sterile base; septa scissile, of hyaline prosenchyma, 14–22  $\mu$  thick; basidia not seen; spores ellipsoid, obtusely pointed, slightly pedicellate, shallowly and finely areolate-reticulate, light brown (sub lente), 8–10 (–11)  $\times$  4.4–5.6 (–7)  $\mu$ .

Australia. September.

Miss Campbell called this fungus a “Violet Puffball.”

AUSTRALIA: Victoria, Melbourne (Lilydale), *F. Campbell 27a* (Mrs. Martin 429) (Kew, Lloyd Mus. 0229, Dodge, and N. Y. Bot. Gard. marked “from Massee Herb.”); South Australia, Mt. Lofty, *J. B. Cleland 13, 14* (Dodge, and Zeller, det. as *Hymenogaster fulvus* Rodw. by Rodway); Adelaide, *J. B. Cleland 784* (Dodge and Zeller).

9. *ARCANGELIELLA STEPHENSII* (Berkeley & Broome) Zeller & Dodge in Dodge, Ann. Mo. Bot. Gard. 18: 463. 1931; E. Fischer in Engler & Prantl, Die Nat. Pflanzenfam. ed. 2, 7a: 32. 1933.

*Hydnangium Stephensii* Berkeley & Broome, Ann. & Mag. Nat. Hist. I. 13: 352. 1844; Quélet, Ench. Fung. 247. 1886; Patouillard, Bull. Soc. Myc. France 30: 348. 1914; Soehner, Zeitschr. f. Pilzk. 2: 153–156. 1923; E. Fischer, Geobot. Inst. Rübel in Zürich, Veröffentl. 3: 573–576. 1925.

*Octaviania Stephensii* Tulasne, Fung. Hypog. 78. 1851; Corda, Icones Fung. 6: 36. 1854; DeToni in Sacc. Syll. Fung. 7: 159. 1888; Lloyd, Myc. Notes 67: 1140. 1922.

*Octavianina Stephensii* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Hydnangium galathejum* Quélet, Ench. Fung. 247-248. 1886; Patouillard, Bull. Soc. Myc. France 26: 199-201. 1910.

*Octaviania galatheja* DeToni in Sacc. Syll. Fung. 7: 491. 1888.

Type: in Kew Herb., British Mus., and Paris.

Fructifications about 2 cm. in diameter, dark rufous drying liver-brown to russet or Hays brown, smooth, rooting base and columella with lactiferous ducts yielding a white milky juice which assumes a reddish tint on exposure to the air but disappears from the cut surface on drying; peridium drying 130-200  $\mu$  thick, composed of gelified, interwoven hyphae, the outer portion more compact, the inner portion filled with lactiferous ducts 6  $\mu$  in diameter; gleba white drying cream-color, finally cinnamon to cinnamon-buff; septa slightly lactiferous, composed of slender hyphae embedded in a gel; spores broadly ellipsoidal to subspherical, with few very fine spines and a thick epispore, 14.5-15.5  $\times$  11-12  $\mu$ .

*H. galatheja* was separated from *H. Stephensii* on its yellow color but it seems to be only a color variation, as microscopically neither Patouillard nor we have been able to separate it.

EXSICCATI: Rabenhorst, Fung. Eur. 1319.

GERMANY: Bayern, Kaufbeurn, E. Soehner 782 (Soehner and Dodge).

FRANCE: L. Quélet (Upsala); Doubs, Hérimoncourt L. Quélet, Aout 1892 (Paris); Besançon, F. Bataille (Dodge); Jura, Lépigny, N. Patouillard, Oct. 1902, 1909 (Farlow); Abbeville, L. Quélet (Upsala); Seine, G. Malençon, 1928 (Dodge) (all French specimens sub *H. galathejum*).

ENGLAND: Leigh Wood, C. E. Broome, distributed in Rabenhorst, Fung. Eur. 1319 (Farlow); near Bristol, C. E. Broome (J. W. Bailey Herb. at Brown Univ.); Bristol, C. E. Broome (Curtis Herb. at Farlow); Clifton, H. O. Stephens & C. E. Broome, 6 Aug. 1843, type (Kew, Brit. Mus., and Paris).

10. *ARCANGELIELLA AFRICANA* (Lloyd) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 365. 1935.

*Octaviania africana* Lloyd, Myc. Notes 67: 1142. 1922.

*Octaviana africana* Verwoerd, S. Afr. Jour. Sci. 22: 164. 1925.

Illustrations: Lloyd, Myc. Notes 67: f. 2172.

Type: in Lloyd Mus. and in Stellenbosch Univ. Herb. 2097.

Fructifications spherical, 1–1.5 cm. in diameter, drying cinnamon-brown to Dresden brown; peridium hard, duplex, the outer layer 150–160  $\mu$  thick, composed of closely woven, slender, hyaline hyphae 1.5–2  $\mu$  in diameter, the inner layer 375–400  $\mu$  thick, composed of hyaline, more loosely woven, septate hyphae 3–4  $\mu$  in diameter, with lactiferous ducts, separable; gleba drying from ferruginous to snuff-brown; septa 15–30  $\mu$  thick, bent, clavate, 25–30  $\times$  7–8  $\mu$ , sterigmata 10–15  $\mu$  long, filiform; spores brown, ellipsoidal, alveolate, slightly foveolate under the alveolae, 15  $\times$  11  $\mu$ , giant spores 18.5  $\times$  15  $\mu$ .

South Africa.

SOUTH AFRICA: Knysna, A. V. Duthie 325, type (Lloyd Mus. 97, Dodge and Zeller).

11. *ARCANGELIELLA BEHRII* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Splanchnomyces Behrii* Harkness, Bull. Cal. Acad. Sci. 1: 30. 1884.

*Hymenogaster Behrii* DeToni in Sacc. Syll. Fung. 7: 174. 1888; Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 249. 1899.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ., in Farlow Herb., N. Y. Bot. Gard. Herb., Lloyd Mus., and Dodge Herb.

Fructifications depressed-globose, 1–4 cm. in diameter, irregularly lobed, pale yellowish drying honey-yellow to isabellacolor, or chestnut-brown to cinnamon-brown; sterile base prominent, pulviniform, cartilaginous; peridium covering the upper half of the fructification, smooth to pulverulent, 85–130  $\mu$  thick, very fragile and peeling badly in sectioning, yellowish, somewhat gelatinous, composed of coarse, yellow hyphae; gleba lemon-yellow, drying cinnamon-brown, cavities large, empty; septa 25–30  $\mu$  thick, yellow to brown, composed of coarse, gelified, nearly parallel hyphae; basidia cylindrical, projecting beyond the hymenium a short distance, mostly 4-spored, sterigmata 5–6  $\mu$  long; spores ellipsoid, ovoid, coarsely and evenly verrucose, with thick epispore, averaging 12  $\times$  8.5  $\mu$ , usually pedicellate, 11–14  $\times$  8–10  $\mu$ , giant spores 14.5–20  $\times$  11–13  $\mu$ ; odorless.



In humus, under *Quercus agrifolia* and *Heteromeles arbutifolia*. Oregon and California. December to March.

The collection by Johnston (219) has quite a few young spores which show a thick epispore, and the distal end almost umbilicate with a very fine, hyaline apiculus projecting from the depression. Very subject to attack by *Sepedonium*.

OREGON: Benton County, Corvallis, S. M. Zeller 8198 (Zeller).

CALIFORNIA: Marin County, H. E. Parks 113 (1918) (Univ. Cal.); Wildwood Glenn, Sausalito, H. W. Harkness, type (Stanford, Farlow, N. Y. Bot. Gard., Lloyd Mus., and Dodge); Alameda County, Berkeley, N. L. Gardner 178 (Univ. Cal., Dodge, and Zeller); Contra Costa County, Richwood Cañon, H. E. Parks 2015 (Dodge and Zeller); Santa Clara County, Call of the Wild, H. E. Parks 291, Guadalupe, H. E. Parks 28, 387, 433 (Z14), 951 (all Univ. Cal., Dodge, and Zeller); San Bernardino County, San Antonio Mts., I. M. Johnston 219 (Lloyd Mus. and Dodge).

11a. var. CAUDATA Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Arcangeliiella caudata* Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 49-52. 1919.

Illustrations: Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 51, f. 1.

Type: in Univ. Cal., Dodge, and Zeller Herb.

Fructifications 0.8-2 cm. in diameter, spherical with attenuate base, flattened or plane above, some quite pyriform, "varying from light brown to a dark yellowish brown or maroon except on a limited area on the under side next to the very short stipe which is almost white" [Gardner], mummy-brown to clove-brown above and clay-color to olive-brown below (in alcohol), surface velvety; peridium 200-300  $\mu$  thick above, very thin or wanting below, sepia under the microscope, composed of radial septate hyphae perpendicular to the surface, forming pseudoparenchymatous tissue having cells about 9-10  $\times$  11-13  $\mu$ , the septa of the hyphae becoming constricted and finally abjointing spherical to oblong oidia-like cells from the surface of the peridium; base sterile, composed of septate, hyaline hyphae 3-5  $\mu$  in diameter, with lactiferous ducts 6-8  $\mu$  broad, more numerous towards the attenuate point which leads to a heavy, branched rhizomorph; rhizomorphs pseudoparenchymatous, brown, supplied with numerous lactiferous ducts; columella

variable from inconspicuous to percurrent, extending to the peridium above, sometimes with lateral branches, concolorous and continuous with the base, the few lactiferous ducts smaller than in the base; gleba fleshy, white or yellowish, drying isabella-color to brownish-olive, exposed near the base in older specimens, cavities small and irregular, somewhat radiating from the base and columella; septa hyaline, consisting of loosely interwoven, hyaline hyphae, few lactiferous ducts, 50–65  $\mu$  broad; cystidia hyaline, large, clavate; paraphyses cylindrical, obtuse, hyaline, septate, 19–20  $\times$  4–5  $\mu$ ; basidia hyaline, slender, clavate, 2–4-spored, 24–26  $\times$  9–13  $\mu$ , sterigmata short, stout, 3–6  $\mu$  long; spores mostly ovoid to ellipsoid, verrucose-rugose, pedicellate, yellow-ochre to ochraceous-tawny, 12–14.5  $\times$  9–11.5  $\mu$ , one large vacuole, exospore thick.

In leaf mould of *Quercus*. Oregon and California. November.

OREGON: Benton County, Corvallis, S. M. Zeller 2005 (Zeller).

CALIFORNIA: Alameda County, Berkeley, N. L. Gardner 219, type (Univ. Cal., Dodge, and Zeller 1623).

12. *ARCANGELIELLA seminuda* (Masse & Rodway) Zeller & Dodge, comb. nov.

*Gymnomyces seminudus* Masse & Rodway, Kew Bull. Misc. Inf. 1898: 125. 1898; Saccardo & Sydow in Sacc. Syll. Fung. 16: 249–250. 1902; Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 56. 1919.

*Octaviania brunneola* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 251. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 248. 1902.

*Arcangeliella brunneola* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Hydnangium McAlpinei* Rodway, Papers & Proc. Roy. Soc. Tasmania 1923: 159. 1924.

*Octaviania microsporium* Mattirollo, herb. nom.

Type: in Kew Herb. Cotype of *O. brunneola* Harkn. in Dudley Herb. at Leland Stanford Jr. Univ. Type of *Hydnangium McAlpinei* in Rodway Herb. at Tasmanian Museum.

Fructifications soft and watery, irregularly spherical, up to

5 cm. in diameter, whitish to muddy brown and ochraceous, drying isabelline, fawn, Natal brown to almost black, 1–2.0 cm. in diameter; sterile base present in young material, wanting at maturity; columella very slender, irregularly developed (arising in two separate places in one specimen) and easily overlooked, composed of closely parallel hyphae loosely interwoven or collapsing into a solid tissue; peridium 500–550  $\mu$  thick when fresh and in preserved material, drying 150–200  $\mu$  thick in the folds to even 50  $\mu$  thick in collapsed portions, outer layer separable, comprising most of the thickness (in the type of *G. semimudus* only half the thickness), composed of strands of more or less parallel hyphae 1.5–3  $\mu$  in diameter, very loosely woven, leaving large lacunae or collapsing on drying in the thinner portions and giving a prosenchymatous appearance, brownish, inner layer 35–40  $\mu$  thick, continuous with the septa and of the same structure, lactiferous ducts occasional throughout, more frequent in the outer portion of the peridium; gleba dense, dark olive-buff becoming avellaneous or army-brown to almost black from spores (warm buff in the type), cavities small, nearly filled with spores; septa 15–40  $\mu$  thick, of slender, interwoven hyphae with lacunae much smaller than those in the peridium except in the angles between the cavities, not otherwise scissile, subhymenium pseudoparenchymatous, lactiferous ducts few; basidia cylindrical, 18–23  $\times$  6–7.5  $\mu$ , soon collapsing; spores spherical or nearly so, very slightly attenuate toward the pedicel, dark brown to black, smooth at first with thick episore which becomes deeply alveolate, easily tearing and appearing unevenly and bluntly echinulate, 12–15  $\times$  11–13  $\mu$ , with about 12 spines per great circle.

In duff under conifers, *Quercus* and *Aesculus*. Pacific coast of North America and Tasmania. January to June in North America (no dates accompanying the Tasmanian material).

It is with some hesitation that we have included all these specimens in the same species. Fundamentally the structure is the same but there is much variation in size, color, and peridial measurements, apparently depending in part on the maturity of the specimen and in part on its subsequent reaction to

processes of drying. The very loose character of the peridium as seen in preserved material allows for a variable amount of collapse on drying. The extremes when first encountered were recognized by us as distinct species, but with the accumulation of material intergrading forms have been seen, until in the present state of our knowledge we have failed to find clear distinctions. It is possible that further field work in Tasmania, Oregon, and California, with more careful relating of immature and mature specimens, may solve some of the problems raised in this group.

OREGON: Benton County, Corvallis, *H. P. Barss* (Zeller 8190); Yamhill County, McMinnville, *S. M. Zeller 2166* (Dodge and Zeller).

CALIFORNIA: Humboldt County, Trinidad, *H. E. Parks 4625* (Zeller); Marin County, Mt. Tamalpais, *H. W. Harkness*, cotype of *O. brunneola* (Stanford); Monterey County, Pacific Grove, *N. L. Gardner (399) & M. B. Nichols* (Univ. Cal. and Zeller); Santa Clara County, San José, *H. E. Parks 960b*, Guadalupe, *H. E. Parks 264, 314, 341, 367, 394, 435, 520, 522, 530, 987, 1125*, Alma, *H. E. Parks 404*, *H. E. Parks & C. W. Dodge 1158*, without locality, *H. E. Parks 1126* (all Univ. Cal., Dodge, and Zeller).

TASMANIA: *L. Rodway 124*, type (Kew); Hobart, *L. Rodway* (Lloyd Mus. 072, and Dodge); Cascades, *L. Rodway 1110* (Dodge); Tasman Peninsula, *L. Rodway 1278* (Dodge); Mt. Nelson, *L. Rodway*, type of *Hydnangium McAlpinei* (Rodway).

### 13. *ARCANGELIELLA PILOSA* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 368. 1935.

Type: in Dodge and Zeller Herbaria.

Fructifications 3–4.5 cm. broad  $\times$  1–4 cm. high, globose to depressed-pyriform, shrinking on drying, at first whitish becoming reddish-brown, drying citrine-drab, light brownish-olive, or olive, smooth, pilose; sterile base prominent, extended above into a branched or plate-like, percurrent columella of loosely interwoven hyphae; peridium 500–1000  $\mu$  thick when fresh, drying 240–320  $\mu$  thick, of a meshy prosenchyma with lactiferous ducts, gelified at maturity, hyaline, the surface layer of erect hyphae 30–40  $\mu$  long and 2–3.5  $\mu$  in diameter, producing a plushy surface (matting down in preserved material); gleba firm, gelified, buff, drying hard and cinnamon to Saccardo's umber, cavities small, empty but collapsing; septa 20–35  $\mu$  thick, of slender, loosely interwoven, gelified (?) hyphae interspersed by a few lactiferous ducts; basidia clavate, 4-spored;

spores hyaline (light yellowish *en masse*), subspherical, minutely alveolate-echinulate, 10–12  $\mu$  in diameter.

In humus soil under oaks. California. February to April.

CALIFORNIA: Santa Clara County, Guadalupe, H. E. Parks, *ith* Z340 type, 524, 525 (Zeller and Dodge).

14. *ARCANGELIELLA ALVEOLATA* (Cooke & Massce) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 365. 1935.

*Octaviania alveolata* Cooke & Massee, Grevillea 16: 2. 1887; Saccardo, Syll. Fung. 9: 280. 1891; Cooke, Handbook Austral. Fungi, 246. 1892; Rodway, Papers & Proc. Roy. Soc. Tasmania 1919: 112. 1920; 1923: 159. 1924.

?*Octaviania Stephensii* var. *nuda* Harkness, Bull. Cal. Acad. Sci. 1. 258. 1885.

*Octavianina alveolata* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Gymnomycetes pallidus* Massee & Rodway, Kew Bull. Misc. Inf. 1898: 125. 1898; Saccardo & Sydow in Sacc. Syll. Fung. 16: 249. 1902; Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 25. 1912; 1923: 160. 1924; Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 55–56. 1919.—not Zeller, Mycologia 4: 197–198. 1922.

*Elasmomyces russuloides* Setchell, Jour. Myc. 13: 240–241. 1907; Saccardo & Trotter in Sacc. Syll. Fung. 2: 467. 1912.

?*Gymnomycetes solidus* Rodway, Papers & Proc. Roy. Soc. Tasmania 1920: 157. 1921; 1923: 161. 1924; Trotter in Sacc. Syll. Fung. 24: 1328. 1928.

*Hydnangium glabrum* Rodway, Papers & Proc. Roy. Soc. Tasmania 1920: 157. 1921; 1923: 157–158. 1924; Trotter in Sacc. Syll. Fung. 24: 1328. 1928.

*Hydnangium Hinsbyi* Rodway, Papers & Proc. Roy. Soc. Tasmania 1923: 158. 1924.

Illustrations: Setchell, Jour. Myc. 13: *pl.* 107.

Type: Cudgegong River, *Hamilton* 514, in Kew Herb. Type of *Gymnomycetes pallidus*, Tasmania, *L. Rodway* 299, in Kew Herb. Type of *Hydnangium glabrum*, Tasmania, slopes of Mt. Wellington, *L. Rodway*, not seen. Material from Cascades, *L. Rodway* 1280 (stated by Rodway to be cotype) in Dodge and Zeller Herbaria. Type of *Elasmomyces russuloides*, Califor-

nia, Alameda County, Berkeley, N. L. Gardner & W. A. Setchell. A specimen so determined in Lloyd Mus. "Herb. Univ. California, Fungi of California 220, *Elasmomyces russuloides* Setchell under *Quercus agrifolia*, Berkeley, N. L. Gardner, Nov. 24, 1904," has been studied by us, and considered to be a portion of the type. Type of *Hydnangium Hinsbyi* from Hobart, L. Rodway, in Rodway Herb. at Tasmanian Museum.

Fructifications subspherical, drying 2 cm. in diameter, pinkish-cinnamon drying walnut-brown to Rood's brown; sterile base prominent and gelified, columella inconspicuous and not well developed; peridium thin, fragile, often flaking off, drying 55–80  $\mu$  thick (only about 40  $\mu$  in the type), composed of slender, periclinal, gelified hyphae; gleba pale red-brown to ochre, drying pinkish-buff; cavities large, subspherical, about 0.2 mm. in diameter; septa thin, 30–40  $\mu$  thick, composed of hyaline, periclinal, gelified hyphae with lactiferous ducts which end in large "gloeocystidia"; basidia early collapsing; spores spherical, girdled by ridges, subreticulate, finely and minutely asperate, 7–9  $\mu$  in diameter, giant spores 10–11  $\mu$ .

Pacific coast of North America, Chile, and Australia.

It is somewhat doubtful whether material from Mt. Wellington and the Cascades, Tasmania, which Rodway referred to *Octaviania alveolata*, is correctly determined, as Rodway states that fructifications were "pale ochre with a dark peridium, gleba dense, waxy, pale ochre becoming dark." This description suggests *Hydnangium compactum* Harkness, but we have seen no material.

OREGON: Linn County, S. M. Zeller 2590, near Peoria S. M. Zeller 2586 (both Zeller).

CALIFORNIA: Marin County, S. Rafael, H. E. Parks 2110 (Univ. Cal. and Dodge); Alameda County, Berkeley, N. L. Gardner 245 (Lloyd Mus. and Dodge), 220 (type of *Elasmomyces russuloides*, Univ. Cal. and Dodge); San Mateo County, Redwood Park, H. E. Parks 2187 (Univ. Cal. and Dodge); Santa Clara County, Saratoga, H. E. Parks 358, 450, 907, 947, 990, 1127; Alma, H. E. Parks 56, N. L. Gardner 508, H. E. Parks, Guadalupe, H. E. Parks 358, 372, 477 (all Univ. Cal. and Dodge); Los Gatos, H. E. Parks 477 (Z27) (Zeller).

CHILE: Concepción (dry hill top), E. Thaxter, Nov. 1904 (Farlow).

AUSTRALIA: Cudgegong R., Hamilton 514, type (Kew); New South Wales, Moona Plains, without collector (Kew); Victoria, without collector 1092 (Kew);

Melbourne, (Lloyd Mus. 0216); *F. Campbell 27b* (Kew); South Australia, Belair, *J. B. Cleland 1*, Mt. Compass, *J. B. Cleland 21*, Mt. Lofly, *J. B. Cleland* (all Dodge).

TASMANIA: *L. Rodway 1277, 299*, type of *Gymnomyces pallidus* (Kew); Cascades, *L. Rodway 1280*, type of *G. glabra* (Dodge and Zeller); Sandfly, *L. Rodway 1107* (Lloyd Mus. and Dodge); Hobart, *L. Rodway* (Lloyd Mus. 088, sub *H. australiense*, and Dodge), *1106* (Lloyd Mus. 075, 0219, as *Hymenogaster violaceus*, and Dodge); unnumbered specimen, type of *Hydnangium Hinsbyi* (Rodway).

15. *ARCANGELIELLA RAVENELII* (Berkeley & Curtis) Dodge, Ann. Mo. Bot. Gard. 18: 463. 1931.

*Octaviania Stephensii* var. *Ravenelii* Berkeley & Curtis in Tulasne, Fung. Hypog. xvii. 1851; Cooke, Grevillea 6: 133. 1873; DeToni in Sacc. Syll. Fung. 7: 159. 1888.

*Hydnangium Stephensii* var. *Ravenelii* Berkeley, Grevillea 2: 33. 1873.

*Hydnangium Ravenelii* Berkeley & Curtis in Curtis, Bot. North Carolina, 110. 1867; Lloyd, Myc. Notes 15: 152. 1903; 41: 569. 1916; Patouillard, Bull. Soc. Myc. France 26: 204. 1910.

*Octaviania Ravenelii* Lloyd, Myc. Notes 67: 1140. 1922.

Type: Ravenel Herb. at Brit. Mus., Berkeley Herb. at Kew, Curtis Herb. at Farlow Herb., and in Upsala.

Fructifications 2.5–4 cm. in diameter, subspherical to pyriform, drying light fawn; sterile base not prominent; columella slender, percurrent with lactiferous ducts which exude a white aromatic milk; peridium 100–180  $\mu$  thick, of gelified, interwoven hyphae with lactiferous ducts 7–8  $\mu$  in diameter; gleba white becoming cream-color; septa 11–15  $\mu$  thick, of slender hyphae in a gel, with lactiferous ducts; basidia clavate, protruding, 1–4-spored, 30–32  $\times$  13–15  $\mu$ , sterigmata very slender, 7–12  $\mu$  long; spores subspherical, alveolate-reticulate, 11–12.5  $\mu$  in diameter, giant spores from 1-spored basidia, 12.5–15  $\times$  15–15.5  $\mu$ .

Partially emergent under leaf mold. Southeastern United States and Oregon.

EXSICCATI: Ravenel, Fung. Carol. II: 71; Fung. Amer. 16; Ellis, N. Amer. Fung. 1211.

WITHOUT LOCALITY: (Lloyd Mus. 52).

SOUTH CAROLINA: Santee Canal, *H. W. Ravenel 883*, type (Brit. Mus., Farlow, Kew, and Upsala); Aiken, *H. W. Ravenel*, in Ellis, N. Amer. Fung. 1211.

GEORGIA: Augusta, *Berry Brown* (N. Y. State Mus. and Zeller 7255).

FLORIDA: *G. Clyde Fisher 12* (Lloyd Mus. 10620); Gainesville, *H. W. Ravenel*, Fung. Amer. 16.

ALABAMA: Auburn, *F. S. Earle* (Lloyd Mus. 0211, 5981, and Dodge); *A. H. Povah 7182, 9080* (in Lloyd Mus., Farlow, Dodge, and Zeller); Spring Hill, *A. S. Bertholet* (Lloyd Mus. 7128, 7182).

OREGON: Corvallis, *S. M. Zeller 2569, 2574* (Zeller).

16. *ARCANGELIELLA SOCIALIS* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 369. 1935.

*Octaviania socialis* Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: 252. 1899; Saccardo & Sydow in Sacc. Syll. Fung. 16: 248. 1902.

Illustrations: Harkness, Proc. Cal. Acad. Sci. Bot. III. 1: pl. 12, f. 5.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications depressed-globose, 1–2 cm. in diameter, or cespitose and coalescing into irregular masses  $2 \times 2.5 \times 4$  cm., surface smooth, cream-color to pinkish, drying clay-color to tawny-olive; sterile base distinct, stipitiform below, continued above as a slender percurrent columella of interwoven hyphae with lactiferous ducts interspersed with islands of pseudoparenchyma; peridium brownish, 220–380  $\mu$ , drying 50–75  $\mu$  thick, composed of polyhedral cells 4–5  $\mu$  in diameter, with very thin walls covered by a thin layer of periclinal hyphae with lactiferous ducts, easily separable; gleba rose-pink drying pinkish-buff (dark brown in alcohol), cavities of medium size and empty; septa 120  $\mu$  thick (drying about 75  $\mu$ ), scissile, composed of large, thin-walled pseudoparenchyma, cells up to 20–25  $\mu$  in diameter; basidia clavate, hyaline,  $20\text{--}30 \times 7\text{--}12$   $\mu$ , 4-spored, sterigmata 7–8  $\mu$  long; spores spherical, hyaline, epispore very finely and shallowly alveolate, 8–15 (–19)  $\mu$  in diameter; odor strongly yeast-like.

Hypogeous under *Eucalyptus*, *Pasania densiflora*, etc. Oregon and California. Winter and spring.

Unfortunately the field notes with *Parks 966* were evidently based on some *Hymenogaster* collected at the same time. We have been unable to trace the notes made on this collection. *Paris 513* is a small, solitary fructification.



OREGON: Benton County, Philomath, *H. M. Gilkey* (Zeller 8189).

CALIFORNIA: *H. E. Parks* 909 (Univ. Cal. and Dodge); Humboldt County, Trinidad, *H. E. Parks* (Univ. Cal. and Dodge); Marin County, San Rafael, *H. E. Parks* 1134, 2070, 2071, 2107, 3036 (Univ. Cal. and Dodge); San Mateo County, Belmont, *H. W. Harkness* 232, cotype (Stanford); Redwood Park, *H. E. Parks* 2180, 2186, 2216 (Univ. Cal., Dodge, and Zeller); Santa Clara County, Aldereroft Creek, *H. E. Parks*, 1167, *C. W. Dodge* 1526, *Alma*, *H. E. Parks* 162 (com. N. I. Gardner 545), Almaden Road, *H. E. Parks* 1132, Guadeloupe, *H. E. Parks* 529, 966, Guadeloupe Mines, *H. E. Parks* 253, 264, 367 (all Univ. Cal. and Dodge); San Jose, *H. E. Parks* 2271, 389 (Univ. Cal., Dodge, and Zeller); Saratoga, *H. E. Parks* 219, 119, 450, 456, 460, 979, 981, 1000, and 2-13-21 (Univ. Cal. and Dodge); Felton Big Trees, *H. E. Parks* 513 (Univ. Cal. and Dodge).

17. *ARCANGELIELLA SCISSILIS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 369. 1935.

Type: in Dodge and Zeller Herbaria.

Fructifications irregular in shape, up to 3 cm. broad; surface very smooth, yellowish drying tawny; columella thin, white, reaching about halfway to the apex; peridium tough, easily cracking off when fresh, drying 320–400  $\mu$  thick, pseudoparenchyma with compact prosenchyma near the surface, and with lactiferous ducts; gleba creamy, drying antimony-yellow, compact; septa 25–35  $\mu$  thick, prosenchyma with lactiferous ducts; spores spherical, very finely and deeply alveolate-echinulate, dark yellowish, 11–15  $\mu$ ; strong odor of witch-hazel (*Hamamelis*).

Coniferous association. Northern California. November.

In this species the peridium is shell-like, easily cracking off, hence the name. The wood rats and pine squirrels eat the fructifications and seem especially fond of the peridium.

CALIFORNIA: Humboldt County, Trinidad, *H. E. Parks* 1125, type (Dodge and Zeller).

18. *ARCANGELIELLA TASMANICA* (Kalchbrenner) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 369. 1935.

*Hydnangium tasmanicum* Kalchbrenner in Massee, Grevillea 19: 95. 1891; Saccardo, Syll. Fung. 11: 172. 1895; Cooke, Handbook Austral. Fungi, 247. 1892; Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 24. 1912.

*Octaviania tasmanica* Lloyd, Myc. Notes 67: 1141–1142. 1922.

*Gymnomyces flavus* Rodway, Papers & Proc. Roy. Soc. Tasmania 1917: 110. 1918; 1923: 161. 1924; Sacc. Syll. Fung. 24: 1328. 1928.

Type: location unknown to us, not found in Kew nor in Berlin.

Fructifications 1-2 cm. in diameter, drying black; fibrils present, adnate, black, scanty; columella probably present (although the specimens available have all been sliced too thin); peridium 140-180  $\mu$  thick, composed of yellowish varicose, vesiculose hyphae, sometimes simulating pseudoparenchyma, 5  $\mu$  in diameter, with latex ducts in the outer portion of the peridium; gleba drying Brussels brown, mottled or marbled by the veins, cavities filled; septa dimorphous, the thicker septa plate-like walls, white, 60  $\mu$  thick, composed of hyaline, varicose, vesiculose hyphae, sometimes pseudoparenchymatous, occasionally with lactiferous ducts, the thinner or true septa 20-30  $\mu$  thick, yellowish, composed of slender, gelified hyphae; spores spherical, 9-14.5  $\mu$  in diameter, dark brown, echinate-tuberculate, with conical spines.

#### Tasmania.

This species is very similar to *A. asterosperma* in tissue structure, color, and color and markings of spores. It differs, however, in size of spores and the more numerous and smaller echinulac. The specimens examined of *Gymnomyces flavus* were young specimens of *A. tasmanica* in which the mature spores were identical with those of the latter.

TASMANIA: Hobart, *L. Rodway* 1379 (Dept. Agr. Victoria [Australia], Lloyd Mus. 090 under *Gymnomyces flavus* Rodw., and Dodge); Wedge Bay, *L. Rodway* 1276, eotype of *Gymnomyces flavus* Rodway (Dodge).

19. *ARCANGELIELLA AUSTRALIENSIS* (Berkeley & Broome) Dodge, Ann. Mo. Bot. Gard. 18: 463. 1931.

*Hydnangium australiense* Berkeley & Broome, Trans. Linn. Soc. London II. Bot. 2: 66. 1883; DeToni in Sacc. Syll. Fung. 7: 176. 1888; Massee, Kew Bull. Misc. Inf. 1898: 128. 1898; Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 25. 1912.

*Octaviania australiensis* Cooke, Handbook Austral. Fungi, 246. 1892; Rodway, Papers & Proc. Roy. Soc. Tasmania 1923: 157. 1924.

*Hydnangium brisbanense* Berkeley & Broome in Cooke, Handbook Austral. Fungi, 247. 1892.

*Secotium sessile* Masee & Rodway in Rodway, Papers & Proc. Roy. Soc. Tasmania 1911: 30. 1912.

*Elasmomyces sessilis* Rodway, Papers & Proc. Roy. Soc. Tasmania 1924: 8. 1925.

Types of both *Hydnangium australiense* and *H. brisbanense* were based on the same specimen, Brisbane, *F. M. Bailey* 188, in Kew Herb. and in British Museum. The type of *Secotium sessile* is Tasmania, *L. Rodway* 647, in Kew, Dodge Herb., and in Lloyd Mus. 0238.

Fructifications subspherical, 2–3 cm. in diameter, pure white drying apricot-buff; stipe short (absent in slice of type available for study), columella vanishing in the gleba; peridium about 100  $\mu$  thick, of very loosely woven, periclinal, hyaline hyphae, separable; gleba light buff, cavities large, empty; septa thin, scissile, 50–60  $\mu$  thick, of slender, gelified hyphae; basidia clavate, soon evanescent; spores spherical, hyaline, 7–8  $\mu$  in diameter.

QUEENSLAND: Brisbane, *F. M. Bailey* 188, type of *H. australiense* and of *H. brisbanense* (Kew and Brit. Mus.).

VICTORIA: *F. Martin* 467 pro parte (Kew); no collector (Lloyd Mus. 0240); E. Gippsland, *F. French*, Jan. 1889 (com. Mueller, Kew); Mallee, *J. Dickson*, 7–10–25 (Dept. Agr. Victoria).

SOUTH AUSTRALIA: Mt. Lofty, *J. B. Cleland* 10, 17 (Dodge and Zeller); S. Yucca, *E. T. Turner* (Lloyd Mus. 11153, Dodge, and Zeller).

TASMANIA: *L. Rodway* 1382 (Dodge and Lloyd Mus. 071); *L. Rodway* 617, type of *Secotium sessile* (Kew, Dodge, and Lloyd Mus. 0329).

NEW ZEALAND: Dunedin, Anderson's Bay, *H. K. Dalrymple* (Weir Herb. 30049).

20. *ARCANGELIELLA KRJUKOWENSIS* (Bucholtz) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 368. 1935.

*Secotium (Elasmomyces) krjukowense* Bucholtz, Hedwigia 40: 314–315. 1901; Материалы къ морфологiи и систематикѣ подземныхъ грибовъ . . . Издвн. Естеств. Ист. Музея Графини Е. П. Шереметевой въ С. Михайловскомъ Московской губ. 1: 142–143. 1902; Ann. Mus. 1: 159. 1903.

Illustrations: Bucholtz, Ann. Mus. 1: pl. 5, f. 8–10; Материалы къ морфологiи и систематикѣ подземныхъ грибовъ . . . Издвн. Естеств. Ист. Музея Графини Е. П. Шереметевой въ С. Михайловскомъ Московской губ. 1: pl. 3, f. 8–10.

Type: Bucholtz Herb. at Farlow, and Berlin.

Fructifications subglobose to irregular, about 3 cm. in diameter, surface smooth, pure white, drying warm buff to buckthorn-brown, lower surface showing groove where peridium reaches the stipe, exposing gleba at maturity; columella percurrent; peridium of interwoven hyphae, with many lactiferous ducts and some islands of pseudoparenchyma, 50–130  $\mu$  thick; gleba orange when fresh, drying clay-color to tawny-olive; septa 40–45  $\mu$  thick, hyaline, with lactiferous ducts composed of loosely interwoven hyphae and islands of pseudoparenchyma, as also in the columella; basidia 2–4-spored; spores 8–11.5  $\mu$ , spherical, citrine-yellow *sub lente*, with short, broadly conic echinulae, young spores sometimes appearing merely asperate.

Hypogeous; caespitose to single. Under *Populus*, *Betula*, and *Tilia*. U. S. S. R. June.

U. S. S. R. [Russia]: Moskva, Krjukovo, *F. Bucholtz*, type (Farlow and Berlin).

20a. var. *MICHAILOWSKJANA* (Bucholtz) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 368. 1935.

*Secotium* (*Elasmonyces*) *michailowskianum* Bucholtz, *Hedwigia* 40: 315. 1901; Материалы къ морфологiи и систематикѣ подземныхъ грибовъ . . . Издап. Естеств. Ист. Музея Графини Е. П. Шереметевой въ С. Михайловскомъ Московской губ. 1: 143–144. 1902; *Ann. Myc.* 1: 171. 1903.

*Elasmonyces michailowskjanus* Saccardo & D. Saccardo in *Sacc. Syll. Fung.* 17: 218. 1905.

Illustrations: Bucholtz, *Ann. Myc.* 1: *pl. 5, f. 11*; Материалы къ морфологiи и систематикѣ подземныхъ грибовъ . . . Издап. Естеств. Ист. Музея Графини Е. П. Шереметевой въ С. Михайловскомъ Московской губ. 1: *pl. 3, f. 11*.

Type: probably in Bucholtz Herb. at Farlow Herb. but not seen.

Fructifications spherical, about 1 cm. in diameter, rufous; columella rather thick, of the same texture as *Arcangeliella krjukowensis*; gleba grayish-ochraceous; cystidia acute; spores and reactions as in that species.

While we have not seen the type of this species, there seems little to distinguish it from *A. krjukowensis*.

21. *ARCANGELIELLA BORZIANA* F. Cavara, Nuov. Giorn. Bot. Ital. N. S. 7: 126. 1900; Saccardo & Sydow in Sacc. Syll. Fung. 16: 256. 1902.

Illustrations: Cavara, Nuov. Giorn. Bot. Ital. N. S. 7: *pl.* 7, *f.* 1-15; Malençon, Trav. dédiés à Louis Mangin, *pl.* 29, *f.* 6.

Type: R. Ist. di Napoli, portion in Dodge and Zeller Herbaria.

Fructifications gregarious, spherical to irregular, oblong, often bilobed,  $0.6-0.8 \times 1.5-3.0$  cm., smooth to pilose, somewhat soft, spotted with yellow; peridium very thin, 70-95  $\mu$  thick, of closely interwoven hyphae, fragile, either lacking or lacerate near the base, slightly lactiferous, latex white, sweet, abundant; gleba light rose-colored, lactiferous; septa of interwoven hyphae, 5-75  $\mu$  thick, base attenuate, sterile; cystidia conical, acute; basidia conspicuous, strongly exserted above the blunt paraphyses, sterigmata 3-4  $\mu$  long, acicular; spores spherical to ellipsoidal, light yellowish, echinulate, 8-11  $\mu$  in diameter, giants 12-13  $\mu$ , episore thick.

In fir forests. Italy. Summer.

The specimen from France is referred here with some doubt as the peridium is lacking and lactiferous ducts are very rare.

ITALY: Trentino, *G. Bresadola*, Julio 1884 (probably Upsala); Etruria, Val-lombrosa, *F. Cavara*, type (R. Ist. di Napoli, Dodge, and Zeller); Lucca, *C. E. Broome* (Brit. Mus. sub. *H. asterospermum*).

FRANCE: Jura, *L. Quélet* (sub *Hydnangium candidum* in Cooke Herb. at Kew).

22. *ARCANGELIELLA CREMEA* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935.

Type: in Dodge and Zeller Herbaria.

Fructifications very irregular in shape, drying subreniform,  $1 \times 2 \times 2$  cm., light buff to cinnamon-buff, marbled; columella percurrent, creamy white; peridium variable, up to 250  $\mu$  thick, of large, thin-walled, periclinal hyphae more or less prosenchymatous, with lactiferous ducts; sterile tissues a mixture of pseudoparenchyma and strands of prosenchyma with lactiferous ducts; gleba firm, cinnamon-buff; septa 120-130  $\mu$  thick, pseudoparenchymatous except for a few large periclinal hyphae in the middle; basidia short-cylindric,  $14 \times 8$   $\mu$ , sterigmata slender, about 4  $\mu$  long; spores spherical, yellow, 9-11  $\mu$

in diameter, alveolate, having about 24 spines per great circle.  
In duff under oak trees. Oregon. March.

OREGON: Benton County, Scott's Hill, south of Corvallis, *E. Sprague*, type (Zeller 7927, and Dodge).

23. *ARCANGELIELLA VULVARIA* (Petri) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 369. 1935.

*Clathrogaster vulvarius* Petri, *Malpighia* 14: 126. 1900; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 250. 1902.

Illustrations: Petri, *Malpighia* 14: *pl. 2, f. 1, 2; pl. 3, f. 2, 3, 5-8, 10, 11, 13.*

Type: in Herb. Bot. Ist. Univ. Firenze.

Fructifications irregular-reniform, about 4 × 6 cm., russet in alcohol (1934), surface irregularly reticulate-sulcate; sterile base scarcely more than a thickening of the peridium; columella conspicuous, fruticose, branching near the base but branches percurrent; peridium 1200-1440  $\mu$  thick in alcohol, composed of densely tangled hyphae without and loose periclinal hyphae within, gelified with abundant large lactiferous ducts 11-12  $\mu$  in diameter; gleba ochraceous-tawny, cavities ovoid, radiating from the columella; septa 110-120  $\mu$  thick, composed of loose, periclinal hyphae with large lactiferous ducts, not so completely gelified; basidia 2-spored, subcylindric, 37-40  $\mu$  long, the upper third collapsing after the separation of the spores, sterigmata short; spores spherical, with short ridges and slender, blunt spines, yellow, 9-12  $\mu$  in diameter.

Sarawak, Borneo, known only from the type collection.

BORNEO: Sarawak, near Sibü, *O. Beccari*, type (Univ. Firenze).

24. *ARCANGELIELLA OCCIDENTALIS* (Harkness) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 368. 1935.

*Octaviania occidentalis* Harkness, *Proc. Cal. Acad. Sci. Bot.* III. 1: 253. 1899; Saccardo & Sydow in *Sacc. Syll. Fung.* 16: 248. 1902.

Illustrations: Harkness, *Proc. Cal. Acad. Sci. Bot.* III. 1: *pl. 42, f. 4.*

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications depressed-globose, 2-2.5 cm. in diameter, 1 cm. high, ochraceous-tawny to buckthorn-brown in alcohol;

stipe 0.4 cm. long, 0.3 cm. in diameter; columella percurrent, 0.1–0.15 cm. in diameter; peridium not enclosing the base, separating from the gleba, up to  $360\ \mu$  thick, composed of interwoven, slender, gelified hyphae; gleba ochraceous-tawny to buckthorn-brown in alcohol, cavities empty, large, irregular; septa  $120\text{--}150\ \mu$  thick, composed of loosely interwoven, gelified, slender hyphae, latex very scant; cystidia mucronate or flask-shaped,  $36\text{--}40 \times 8\text{--}10\ \mu$ ; paraphyses truncate, clavate, septate; basidia  $52 \times 5\text{--}6\ \mu$ , clavate, sterigmata short; spores hyaline to slightly yellowish,  $11\text{--}12\ \mu$  in diameter, spines acicular, short, numerous.

California, March.

CALIFORNIA: Placer County, Whe Bridge, *H. W. Harkness 137*, cotype (Stanford).

25. *ARCANGELIELLA ROSEA* (Harkness) Zeller & Dodge in Dodge, Ann. Mo. Bot. Gard. 18: 462. 1931.

*Octaviania rosea* Harkness, Bull. Cal. Acad. Sci. 1: 29. 1884; Proc. Cal. Acad. Sci. Bot. III. 1: 252. 1899; DeToni in Sacc. Syll. Fung. 7: 160. 1888.

*Octavianina rosea* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Hydnangium Soderstroemii* Lagerheim in Patouillard & Lagerheim, Bull. Soc. Myc. France 9: 142. 1893; Saccardo, Syll. Fung. 11: 172. 1895.

*Arcangeliella Soderstroemii* (Lagerh.) Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 52. 1919.

*Hydnangium pallidum* Lloyd, Myc. Notes 65: 1031. 1921.

*Octaviania pallida* Lloyd, Myc. Notes 67: 1140. 1922.

*Octaviania Stillingeri* Lloyd, Myc. Notes 67: 1140. 1922; Rick, Egatea 14: 111. 1934.

Illustrations: Lloyd, Myc. Notes 65: *pl. 171, f. 1867*.

Type: cotypes in Dudley Herb. at Leland Stanford Jr. Univ., Lloyd Mus., Farlow, and Mo. Bot. Gard. Herbaria. Type of *H. Soderstroemii* in Stockholm, Upsala, Berlin, Patouillard Herb. at Farlow Herb., and Lloyd Mus. Type of *H. pallidum* in Lloyd Mus. and Dodge Herb. Type of *O. Stillingeri* in Lloyd Mus. and Dodge Herb.

Fructifications depressed-globose to pyriform, 2–3.5 cm. in

diameter, pinkish or pale rose when fresh, drying ashy or buckthorn-brown to isabella-color; sterile base attenuate, short or inconspicuous; columella rudimentary or percurrent, confluent with the peridium above, always very thin; peridium smooth and persistent above, evanescent below, early breaking away from the sterile base, 50–80  $\mu$  thick, of large-celled pseudo-parenchyma with large superficial hyphae giving a silkiness to the surface; gleba pale, drying chamois to isabella-color or grayish, fragile, cavities relatively large, mostly radiating from the base and columella; septa thin, fragile, drying about 40  $\mu$  thick, of loosely woven, often gelified hyphae with lactiferous ducts; basidia mostly 2-spored, subcylindrical, 40–60  $\times$  6–10  $\mu$ ; sterigmata stout, conical, 6–10  $\mu$  long; spores subspherical, oblate below, pedicellate, rather finely echinulate (about 20 to the circumference), 11–17  $\mu$  in diameter, giant spores 17–19  $\mu$ , with coarser conical spines, thick episporium; latex white.

Mostly hypogeous in coniferous woods. Pacific Coast of United States and South America. Spring and autumn.

OREGON: Benton County, Corvallis, *S. M. Zeller 2559* (Zeller).

CALIFORNIA: Alameda County, Berkeley, *H. E. Parks 995*, 1967, 1967a, 1967b (Dodge and Zeller); San Francisco, Golden Gate Park, *H. W. Harkness 117*, cotype (Stanford, Lloyd Mus., 0232, Mo. Bot. Gard. 5638, and Farlow), *C. E. Stillinger*, type of *O. Stillingeri* (Lloyd Mus., Dodge, and Zeller); Ingleside, *N. L. Gardner 209* in part (Univ. Cal., Dodge, and Zeller); Parnassus Heights, Suto Woods, *E. H. Kelley* (com. N. L. Gardner 22, Univ. Cal., Dodge, and Zeller); *W. A. Setchell & C. C. Dobie* (com. N. L. Gardner 25, Univ. Cal.); Santa Clara County, Saratoga, *H. E. Parks 1014*, 2161, Guadalupe, *H. E. Parks 393*, San José, St. James Park, *H. E. Parks 371*, 376, (Z30), 389, 393, 957, *Zeller 1666* (*H. E. Parks*) (all Univ. Cal., Dodge and Zeller).

ECUADOR: Quito, *L. Soderstrom & Lagerheim*, 1891, 1892, type of *H. Soderstromia* (Stockholm, Upsala, Berlin, Farlow, Lloyd Mus. 6395, Dodge, and Zeller); *L. Mille 3*, type of *H. pallidum* (Lloyd Mus. 12127, Dodge, and Zeller).

BRAZIL: *J. Rick 325* (Lloyd Mus., and Dodge).

26. *ARCANGELIELLA ASTEROSPERMA* (Vittadini) Zeller & Dodge, *Ann. Mo. Bot. Gard.* 22: 366. 1935.

*Octaviania asterosperma* Vittadini, *Monogr. Tuberac.* 17. 1831; Tulasne, *Ann. Sci. Nat. Bot.* II. 19: 276. 1843; *Fung. Hypog.* 77–78. 1851; Berkeley & Broome, *Ann. & Mag. Nat. Hist.* I. 18: 76. 1846; Corda, *Icones Fung.* 6: 35–36. 1854; Winter in Rabenhorst, *Krypt.-Fl. Deutschl.* 1: 878. 1883; De-



Toni in Sacc. Syll. Fung. 7: 159. 1888; Massee, Ann. Bot. 4: 31. 1889 [often cited as Monogr. Brit. Gast.]; Hesse, Hypog. Deutschl. 1: 72-74. 1891; Boudier, Icones Myc. 4: 97-98. 1905-1910; Hollós, Magyar. Földalatti Gombai, 95-96, 206-207. 1911; Patouillard, Bull. Soc. Myc. France 30: 347-348. 1914; Lloyd, Myc. Notes 67: 1143. 1922 (pro parte).

*Hydnangium asterospora* Quélet, Mém. Soc. d'Émulation de Montbéliard 4: 368. 1873 [often cited as Champ. du Jura et des Vosges 2]; Ench. Fung. 248. 1886.

*Octaviania mutabilis* Roumeguère, Rev. Myc. 7: 23. 1885; DeToni in Sacc. Syll. Fung. 7: 159-160. 1888; Bucholtz, Bull. Soc. Imp. Nat. Moscou N. S. 21: 485-486. 1908.

*Octaviania brunnea* Hesse, Hypog. Deutschl. 1: 78-79. 1891; Sacc. Syll. Fung. 11: 169. 1895.

*Octavianina asterosperma* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Octavianina brunnea* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.

*Octavianina mutabilis* O. Kuntze, Rev. Gen. Pl. 3<sup>2</sup>: 501. 1898.  
—not *Octaviania mutabilis* Hesse, Hypog. Deutschl. 1: 77. 1891.

*Octaviania asterospora* Th. M. Fries, Svensk Bot. Tidskr. 3: 272-273. 1909; Th. C. E. Fries, Ark. f. Bot. 17<sup>o</sup>: 12. 1922.

Illustrations: Baillon, Dict. 1: 745, f. 4; Boudier, Icones Myc. 1: pl. 191; Cooke, Handbook Brit. Fung. 1: 355; Corda, Anleit. z. Stud. Myc. pl. D, f. 45: 5-6; Fourquignon, Champ. Supér. 123, f. 94; Hesse, Hypog. Deutschl. 1: pl. 3, f. 1-7; pl. 5, f. 15; pl. 6, f. 4; Luerissen, Syst. d. Bot. 262, f. 11; Payer, Bot. Crypt. 114, f. 529; Quélet, Mém. Soc. d'Émulation de Montbéliard 4: pl. 4, f. 3 [often cited as Champ. du Jura et des Vosges 2]; Roumeguère, Cryptog. Illustr. f. 374; Smith, Brit. Basid. 487, f. 140; Swanton, Fungi, pl. 17, f. 9-11; Tulasne, Ann. Sci. Nat. Bot. II. 19: pl. 17, f. 21; Fung. Hypog. pl. 11, f. 1; Vittadini, Monogr. Tuberac. pl. 3, f. 7; pl. 5, f. 9a; Winter in Rabenhorst, Krypt-Fl. Deutschl. ed. 2, 1: 871.

Type: Material from Vittadini in Brit. Mus. and in Paris. Type of *O. mutabilis* distributed in Roumeguère, Fung. Sel. Gall. Exsicc. 3159, a copy in Farlow Herb., also cotype ex herb. Bommer in Lloyd Mus. Type of *O. brunnea* in Upsala.

Fructifications subspherical to reniform, up to  $5 \times 3.5$  cm.; surface tubercular-verrucose, pulverulent, with numerous fibrils, pure white with pinkish flecks which disappear, becoming greenish passing to deep olive, dirty brown to the touch, avellaneous or warm sepia to wood-brown or bister in alcohol, drying cinnamon-buff to sepia or even black; sterile base pulvinate to palmate in vertical section, prosenchymatous with hyaline lactiferous ducts, on drying prosenchyma partially collapsing; peridium 320–480  $\mu$  thick, drying 150–200  $\mu$ , hyphae with vesiculose cells on the outside, within prosenchyma of large, vesiculose cells and relatively few lactiferous ducts; gleba white, exuding a salmon-tinted milk, brownish turning blue-black on exposure, becoming warm sepia in alcohol, and drying cinnamon-brown to Prout's brown or snuff-brown; cavities comparatively large, more or less radially arranged, filled with spores; septa hyaline, prosenchymatous, of large, vesiculose cells often appearing pseudoparenchymatous, with lactiferous ducts, the larger, plate-like septa 110–150  $\mu$  (drying 75–100  $\mu$ ) thick, the smaller septa 30–35  $\mu$  (drying 20–25  $\mu$ ) thick; basidia short, clavate, 20–22  $\mu$  long, 4-spored, sterigmata 5–6  $\mu$  long; cystidia fusiform, 50–60  $\times$  13–14  $\mu$ ; spores spherical, thickly covered with large conical to pyramidal spines 2  $\mu$  long, 13–16  $\mu$  in diameter including the spines, warm sepia; odor of acrid meal; latex salmon-color.

Europe and eastern North America.

The texture, the dark color of the spores, and the spore-filled cavities apparently led Vittadini to include this species in his genus *Oclaviania* (*Melanogaster* Corda) where it was sharply distinguished from the other species of the genus by its star-shaped spores.

EXSICCATI: Roumeguère, Fung. Sol. Gall. 3159; Rabenhorst, Fung. Eur. 1277.

SWEDEN: Stockholm, L. Romell, 1912 (Upsala).

DENMARK: Munkebjerg, H. Jensen, 1888 (Upsala); Mosn, Lisslund, F. Rosenkrantz, 25 Aug. 1900 (Upsala).

CZECHOSLOVAKIA: Boehmerwald, Arber, 200 m., Soehner 773 (Soehner and Dodge).

GERMANY: Marburg, R. Hesse, 1886, 1 July, 1890, type of *O. brunnea*, Aug. 19, 1891, 1901 (Upsala); Altmorschen, R. Hesse, 29 March, 1900; also Altmorschen, R. Hesse, sub. *O. brunnea* (both Farlow).

ITALY: Lombardia, near Milano, *C. Vittadini*, type (Brit. Mus., Paris); Lucca, *C. E. Broome*, Sept. 1846, and spec. no date (Brit. Mus.).

ALGERIA: Oran, *without collector* (Kew).

FRANCE: Ardennes, Florenville, *E. Bommer & M. Roussseau*, type of *O. mutabilis* in Roumeguère, Fung. Sci. Gall. Exsicc. 3159 (Farlow, also specimen ex herb. Bommer in Lloyd Mus. and Dodge); Seine-et-Oise, Montmorency, *E. Boudier* (Lloyd Mus. 5339, and Dodge); Loiret, Gien, *Tulasne*, 1843 (Paris); Loire-et-Cher, Mer, *N. Patouillard* (Farlow); Jura, Lépimay, *N. Patouillard*, Aug. 1913 (Farlow); *L. Quélet* (Upsala); Vandoucourt, *L. Quélet* (Upsala).

ENGLAND: Cornwall, Boconnoc, near Lostwithiel, *C. E. Broome*, Oct. 1848, Oct. 1849 (Brit. Mus.); Devonshire near Chudleigh, Oct. 1845, *C. E. Broome* (Brit. Mus.); *C. E. Broome* (Farlow); ex herb. J. Ralfs (Brit. Mus.); Wiltshire, Bowood, *C. E. Broome*, Oct. 1863 (Brit. Mus., Kew, and Upsala); Hampshire, Lyndhurst, *C. E. Broome*, (Brit. Mus. and Kew).

NEW YORK: Michigan Hollow, near Ithaca, *H. M. Fitzpatrick* 9969, 25 Sept., 1926 (Dodge and Zeller 1543).

MICHIGAN: Ann Arbor, *C. H. Kauffman*, 2 Oct. 1892, *B. B. Kanouse* (both Univ. Mich., Dodge, and Zeller).

NORTH CAROLINA: Cranberry, *E. Thaxter B3H* (Farlow).

TENNESSEE: Burbank, *E. Thaxter B2, H 1* (Farlow).

26a. var. *DEPAUPERATA* (Tulasne) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Octaviania asterosperma* var. *depauperata* Tulasne, Fung. Hypog. 78. 1851.

*Octaviania vacua* Tulasne, herb. nom.

Illustrations: Tulasne, Fung. Hypog. *pl. 11, f. 2*.

Type: Tulasne Herb. at Paris.

This variety differs from the species in having almost no sterile base, basidia linear, obtuse, spores subobovate, appearing transversely striate, rugulose and appendiculate.

Under fallen leaves of *Quercus suber*. Southern France. December to January.

*Gymnomyces vesiculosus* Coker & Couch, Gast. Fl. United States & Canada, 23. *pl. 16, 17, 105*. 1928, may belong here but no material has been seen.

FRANCE: Var, Hyères, *Tulasne*, Dec. 1844, type (Paris).

26b. var. *HOLOLEUCA* (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Octaviania asterosperma* var. *hololeuca* Hesse, Hypog. Deutschl. 1: 74. 1891.

Type: location unknown to us, but specimens labeled *Oc-*

*taviana asterosperma* var. from Marburg, collected and determined by R. Hesse, at Farlow Herb. and at Upsala, agree with Hesse's description in having very small cavities and a thick, silky, white peridium.

Fructifications large, 3–4 × 2–2.5 cm., depressed-globose to reniform; surface felty-fibrillose, light buff to Prout's brown (in alcohol) to Mars brown where touched; peridium 900–1500  $\mu$  thick, stupose, of loosely woven, brownish hyphae, about 3  $\mu$  in diameter, consistency of felt; sterile base prominent, of large white hyphae, up to 8  $\mu$  in diameter; gleba clay-colored to tawny-olive in younger specimens to hazel and Prout's brown in larger specimens, veins large, white; cavities rather large, becoming filled with spores; septa thick, 85–140  $\mu$  thick (80–100  $\mu$  not including hymenia), of hyaline, stupose, interwoven hyphae about 3  $\mu$  in diameter; basidia 2–4-spored, 19–22 × 8  $\mu$ ; spores 11–14  $\mu$  in diameter (15–18  $\mu$  with echinulae), appendiculate, dark brown, warted with large echinulae, about 8–12 to the periphery.

GERMANY: Marburg, R. Hesse, type (Farlow, under the name *Octaviana asterosperma* Vitt. var.).

27. ARCANGELIELLA BECCARI (Petri) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

*Clathrogaster Beccari* Petri, Malpighia 14: 126. 1900; Sacc. & Sydow in Sacc. Syll. Fung. 16: 250. 1902.

Illustrations: Petri, Malpighia 14: pl. 2, f. 3–5, 7–9.

Type: in Bot. Ist. Univ. Firenze and Dodge Herb.

Fructifications spherical to reniform, 1–3 cm. in diameter, raw sienna in alcohol [1934], surface smooth; no sterile base nor columella evident; peridium about 640  $\mu$  thick in alcohol, composed of densely tangled hyphae without, and loose periclinal hyphae within, embedded in a gel with lactiferous ducts 7–8  $\mu$  in diameter, relatively straight; gleba amber-brown, cavities elongate, radiating from the base which is scarcely more than a thickened peridium; septa about 110  $\mu$  thick, the inner 30–40  $\mu$  thick, similar to the inner peridium in structure; basidia clavate, 2-spored, about 80 × 11  $\mu$ , only the outer half collapsing after the separation of the spore, sterigmata short;

spores 11–15  $\mu$  in diameter, spherical with very high ridges, irregularly disposed over the surface, yellow.

Sarawak, Borneo, known only from the type locality.

This species is closest to *A. Gardneri* in spore markings but differs in the spherical spores, thicker peridium, much larger basidia and spores.

BORNEO: Sarawak, Sibü, *O. Beccari*, type (Dodge and Univ. Firenze).

#### MACOWANITES

*Macowanites* Kalchbrenner, *Grevillea* 10: 107. 1882; DeToni in *Sacc. Syll. Fung.* 7: 179. 1888; E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam.* I. 1<sup>st</sup>: 200–300. 1899; Zeller & Dodge, *Ann. Mo. Bot. Gard.* 6: 56–59. 1919.

*Macowania* Kalchbrenner, *Gardeners' Chron.* N. S. 5: 785. 1876.—*non Macowania* Oliver in Hooker, *Icon. Pl.* III. 1: 49. 1870.

The type species of the genus is *Macowanites agaricinus* Kalchbrenner.

Fructifications subspherical when young, pileate at maturity, epigeous, stipitate, fleshy; peridium covering the top of the pileus only; gleba covering the under surface of the pileus, free to decurrent, composed of irregular anastomosing cavities, more or less radiating from the stipe; basidia 2-spored; spores spherical, echinulate.

1. *MACOWANITES AGARICINUS* Kalchbrenner, *Grevillea* 10: 107. 1882; DeToni in *Sacc. Syll. Fung.* 7: 179. 1888; Lloyd, *Myc. Notes* 7: 1198. 1923; Zeller & Dodge, *Ann. Mo. Bot. Gard.* 6: 58–59. 1919; Verwoerd, *S. Afr. Jour. Sci.* 22: 166. 1925.

*Macowania agaricina* Kalchbrenner in *Gardeners' Chron.* N. S. 5: 785. 1876.

Illustrations: Kalchbrenner, *Gardeners' Chron.* N. S. 5: 785, *f.* 141; E. Fischer in Engler & Prantl, *Die Nat. Pflanzenfam.* I. 1<sup>st</sup>: *f.* 148; Lloyd, *Myc. Notes* 7: *pl.* 245, *f.* 2455, 2456.

Type: South Africa, *MacOwan* 1211, a slice lacking one corner (which is in N. Y. Bot. Gard.) at Kew, a slice in Upsala; two water-color drawings (reproduced in the 'Gardeners' Chronicle') at Kew, showing pileus buffy brown, gleba isabella, stipe

white with cut surface cartridge-buff or a little darker below. These drawings seem to have been based on another specimen, perhaps the one in Upsala, which is much less expanded.

Fructifications hemispheric when young becoming deep infundibuliform, resembling *Cantharellus floccosus* in habit (judging from the dried slice), pileus drying Sayal brown, flesh thick about the depression, abruptly thinning beyond the disc; peridium continuous over the top of the pileus, about  $30\ \mu$  thick, of compact, thick-walled, periclinal hyphae, flesh of large, loosely woven, thin-walled hyphae with lactiferous ducts; stipes short, merging into the flesh of the pileus, sometimes resembling the tissues in the stipe of *Lycoperdon*, drying Sayal brown; gleba decurrent, deep olive-buff with snuff-brown septa, cavities contorted, empty, open below; septa variable in thickness, similar to the flesh in texture; basidia clavate, 2-4-spored, soon collapsing; spores ellipsoidal to subspherical, echinulate, asymmetrically placed on the sterigma as in the *Hymenomyces*, 11-12  $\mu$  in diameter.

Known only from the type collection.

SOUTH AFRICA: Somerset East, MacOwan 1911, type (Kew and Upsala).

2. *MACOWANITES MAGNUS* Parks in Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 369. 1935.

Type: in Univ. Cal. Herb.

Fructifications 3-14 cm. broad, resembling a stout agaric or *Boletus*, cap irregular, at first conic then expanded and almost plane, margins irregular to sinuate, surface smooth, viscid, pale tan to dark brown when fresh, drying fawn-brown to army-brown or cinnamon-buff; stipe short, thick, central, up to 3 cm. thick, 3-7 cm. long, white, brittle, hollow-stuffed, bulbous at base, abruptly attenuated below bulb, subglabrous to innate-fibrillose, homogeneous inside, of longitudinal, meshy fibrillae of fine hyphae; gleba white at first, drying warm buff with vinaceous tints, spongy as in *Gautieria morchelliformis*, expanded, more or less radiating from the center of the pileus, free to adnexed, exposed below, covered by a peridium above, cavities large, labyrinthiform; peridium duplex, about 250-380  $\mu$  thick, inner layer 150-250  $\mu$  thick, loosely stipose with ropy strands

of fine hyphae, outer layer 70–120  $\mu$  thick, compact, stupose, of gelified hyphae, viscid; septa averaging 170  $\mu$  thick including hymenia (about 95  $\mu$  between hymenia), stupose in central portion, subhymenia pseudoparenchymatous; basidia large, cylindric to subclavate, 2-spored, projecting above paraphyses, 10–11  $\times$  20–24  $\mu$ ; paraphyses cylindric, 4–6  $\times$  30–50  $\mu$ ; sterigmata short; spores subspherical, spines short, fine, 7.5–10  $\mu$  in diameter, hyaline; odor and taste like a mild *Lactarius*, becoming pungent and offensive in age.

Partially covered by leaves, under various kinds of trees. Oregon and California. October and November, and May.

Because of the lactiferous ducts in the sterile tissues this species may be considered close to *Arcangeliella*.

In the Oregon collections the surface is even, shiny-glabrous, interspersed with tiny squamules, avellaneous; gleba cream color; stipe white to cream-color, squamulose above.

OREGON: Lincoln County, near Agate Beach Inn, S. M. Zeller & A. H. Smith (Zeller 8235); Yachats, S. M. Zeller 8239 (Zeller).

CALIFORNIA: Santa Clara County, Call of the Wild, H. E. Parks 203, type (Univ. Cal, Dodge, and Zeller 2804).

# MELANOGASTER<sup>1</sup>

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Owing to pressure of other work, there seems little opportunity for further study of the Hymenogasteraceae (*sensu latiore*) in the near future; consequently it seems well to present *Melanogaster* at this time without the small related genera of which we have seen little or no material. While the common European species are well represented in the larger herbaria, there are several species of doubtful affinity of which the types have been lost and which are known to us only from the original descriptions. We have included these, however, in the hope that they may be again encountered.

As in previous papers, we have used the same color standards and cited the specimens studied with the same abbreviations. For financial assistance we are grateful to the American Association for the Advancement of Science (grant in 1923 to the senior author), to the John Simon Guggenheim Memorial Foundation which appointed the junior author a fellow to Europe in the autumn in 1930, and to the Science Research Fund of Washington University (grant of 1933 to the junior author).

## MELANOGASTER

*Melanogaster* Corda in Sturm, Deutschl. Fl. III. 19: 1. 1831; Icones Fung. 5: 23. 1842.

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Issued January 8, 1937.



*Bullardia* Junghuhn, *Linnaea* 5: 408. 1830.—*non Bulliarda* Necker, *Elem.* 2: 321. 1790; DC. *Bull. Soc. Philomath.* 3: 1. 1801.

*Octaviana* Vittadini, *Monogr. Tuberac.* 15–20. 1831.

*Argyllum* Wallroth, *Fl. Cryptog. Germ.* 2: 874. 1833.

*Hymenogaster* Endlicher, *Gen. Pl.* 30. 1836.—*non al.*

?*Uperhiza* Bosc, *Ges. Naturf. Freunde Berlin Mag.* 5: 88. 1811 (without species name); Nees, *Syst. d. Pilze* 1: 159; 2: 41, pl. 15, f. 146. 1816 (as *U. carolinensis*).

?*Uperrhiza* Fries, *Syst. Orb. Veg.* 1: 135. 1825.

?*Hyperrhiza* Sprengel in Linné, *Syst. Veg.* ed. 16, 4: 416. 1827.

The type of *Melanogaster* is *M. tuberiformis* Corda. *Bullardia* was based on *B. inquinans* Jungh., usually considered a synonym of *M. variegatus* (Vitt.) Tul. *Bullardia* has universally been considered a variant spelling of *Bulliarda* and hence preoccupied. We have not seen type material, and prefer to regard it as a permanent source error. We have not recognized the specific epithet, *B. inquinans*, following the universal practice of the last century. *Octaviana* was based on *Octaviana variegata* Vitt. *Argyllum* Wallr. is based on *Bullardia inquinans* Jungh. *Uperhiza* and its variant spellings are all based on *U. carolinensis* Nees. This genus name was frequently used up to 1844 as a synonym of *Melanogaster* and of course antedates it. A careful reading of the Bosc and the Nees descriptions suggests that this is rather a species of *Scleroderma* but it is too poorly described to place in the absence of type specimens which have evidently been lost for at least a century. It seems unwise to overturn the nomenclature of the greater part of a century when, in the absence of adequate description or type, it may become a permanent source of confusion. We hereby recommend that *Melanogaster* be conserved against *Uperhiza* and its variant spellings, *Uperrhiza*, and *Hyperrhiza*.

Fructifications subspherical to irregular, usually brownish to blackish, at least at maturity, surface even, dull, usually with strong odors; fibrils usually present, often inconspicuous; peridium mostly prosenchymatous, sometimes with vesiculose cells, often not well differentiated from the septa of the gleba,

not separable; gleba usually dark brown becoming black in age with tendency to deliquesce, with whitish septa which may become discolored yellowish or reddish on wounding or in age, cavities filled by a gel containing the evanescent basidia and the spores; septa of gelified prosenchyma, often with traces of the fundamental tissue; basidia mostly clavate, evanescent, scattered throughout the gel of the cavities, borne singly on branching hyphae, 4–8-spored, sterigmata short and often very broad, so that the spores appear sessile on the basidium; spores brown, occasionally yellow, variable in shape from subspherical to subcylindric, usually with a thick episore.

Confined to the more humid portions of the north temperate zone, except for one species from the mountains of Northern India and one species in New Zealand.

#### KEY TO THE SPECIES OF MELANOCASTER

1. Spores averaging more than 11  $\mu$  in length..... 2
1. Spores averaging less than 11  $\mu$  in length..... 5
  2. Spores citriform to almost fusiform, sometimes bluntly apiculate.....
    - .....1. *M. ambiguus* (p. 642)
  2. Spores obovoid..... 3
3. Spores large, 15–18  $\mu$  long..... 3. *M. macrosporus* (p. 644)
3. Spores smaller..... 4
  4. Spores 11–13  $\times$  7.4–8  $\mu$ ..... 3. *M. intermedium* (p. 645)
  4. Spores 10–11.5  $\times$  5.5–7  $\mu$ ..... 4. *M. tuberiformis* (p. 645)
5. Spores 10–11  $\mu$  long..... 6
5. Spores shorter..... 7
  6. Spores more than 7  $\mu$  broad..... 1a. *M. ambiguus* var. *euryspermus* (p. 643)
  6. Spores 5.5–7  $\mu$  broad..... 4. *M. tuberiformis* (p. 645)
7. Spores small, less than 5  $\mu$  long..... 5. *M. microsporus* (p. 646)
7. Spores longer..... 8
  8. Spores oblong to cylindrical..... 9
  8. Spores ellipsoid, ovoid, or subspheroid..... 10
9. Spores definitely truncate below, 6–8.4  $\times$  3.5–4  $\mu$ , rather dark *sub lente*.....
  - ..... 6. *M. Broomeianus* (p. 647)
9. Spores rounded at both ends, 8–9.6  $\times$  5.5–6.5  $\mu$ , almost hyaline *sub lente*.....
  - ..... 7. *M. rubescens* (p. 648)
10. Gleba drying brown or brownish-black, spores rather dilute brown or yellowish..... 11
10. Gleba drying black, spores dark brown, ellipsoid or obovoid..... 12
11. Spores broadly ovoid or subspheroid, 8–9.6  $\times$  6.7–7.7  $\mu$ ..... 8. *M. Parksi* (p. 649)
11. Spores ovoid, ellipsoid to fusiform, somewhat truncate below, 8–9.6  $\times$  5.5–6  $\mu$ .....
  - ..... 7. *M. rubescens* (p. 648)
  12. Spores less than 4  $\mu$  broad, 5.5–6.7  $\times$  2–3.7  $\mu$ ..... 9. *M. mollis* (p. 650)
  12. Spores 4  $\mu$  or more broad..... 13

13. Spores truncate,  $6-8 \times 4-5 \mu$ , exospore conspicuous... 10. *M. durissimus* (p. 650)  
 13. Spores not truncate,  $7.5-10.3 \times 5-7.5 \mu$ , exospore not conspicuous.....  
 ..... 11. *M. variegatus* (p. 651)

1. *MELANOASTER AMBIGUUS* (Vittadini) Tulasne, Ann. Sci. Nat. Bot. II. 19: 378. 1843.

*Octaviania ambigua* Vittadini, Monogr. Tuberac. 18. 1831.

*Hyperrhiza liquaminosa* Klotzsch in Dietrich, Fl. Reg. Boruss. [Fl. Königr. Preuss.] 7: no. 468. 1839.

*Argyrium liquaminosum* Wallroth, Fl. Cryptog. Germ. 2: 874. 1833.

*Melanogaster Klotzschii* Corda, Icones Fung. 5: 23. 1842; Anleit. z. Stud. Myc. 95. 1842.

Illustrations: Vittadini, Monogr. Tuberac. pl. 4, f. 7.

Type: location unknown to us but specimen so determined in Broome Herb. at British Museum. *Argyrium liquaminosum* from Thüringen, Wallroth.

Fructifications subspherical to ellipsoidal, 1-3.5 cm. in diameter, pale olive to olivaceous-brown when fresh, becoming cinnamon-brown to Prout's brown on drying, surface cottony-furfuraceous, fibrils scanty, inconspicuous; peridium 300-600  $\mu$  thick when fresh, somewhat thinner in old dry material, hyaline within, yellowish-brown toward surface, prosenchymatous, homogeneous, with outer filaments fraying out to form the more or less erect, brown tomentellum at the surface, of large, thick-walled, agglutinated hyphae which often collapse on drying; gleba black with yellowish septa, fundamental tramal tissue of more slender, smaller-celled prosenchyma, cavities filled with spores embedded in a gel; basidia clavate, evanescent, mostly 4-spored; spores (8-) 12-16 (-17)  $\times$  (5.5-) 6-8 (-8.5)  $\mu$ , obovoid with more or less acute apex, approaching citriform, thick-walled, smooth, very often uniguttulate, dark brown when mature.

Under hardwoods. Central and western Europe, New York, Kentucky, Oregon, and New Zealand. April to October.

The specimen (Zeller Herb. 2338) collected by Dr. Helen M. Gilkey along Greecy Creek, Benton Co., Oregon, differs enough from *M. ambiguus* for us to refer it here with some doubt. The peridium in the one fructification has an outer white layer

(50–60  $\mu$  thick) which darkens when bruised as described for *M. aureus*. The inner peridium is dark brown (150–170  $\mu$  thick). The spores are as in *M. ambiguus*, but the cavities are filled with a meshy growth of hyphae bearing the basidia with no evidence of gelification.

GERMANY: Preussen, Neu Schöneberg bei Berlin, *F. Klotzsch*, type of *Hyperhiza uquantinosa* (Kew, Paris); Marburg, *E. Hesse*, 1885 (Farlow).

ENGLAND: Bristol, *C. E. Broome 355* (Brown Univ.); King's Lynn, *C. B. Plowright 503* (Brit. Mus., Stanford).

FRANCE: *L. Quillet* (Upsala); Seine, Bois de Boulogne, July 9, 1843, *L. Tulasne* (Paris).

ITALY: near Milano, *C. Vittadini* (Brit. Mus.).

NEW YORK: Syracuse, *L. H. Pennington* (Lloyd Mus. 87, and Dodge).

KENTUCKY: High Ridge, *C. O. Mattingly & F. T. McFarland* (Zeller).

OREGON: Benton County, Alsea Road, *H. P. Barss* (Zeller 681), *H. M. Gilkey* (Dodge, and Zeller 2338, 2803, 2805); Corvallis, *L. M. Booser* (Dodge and Zeller 2285); Kings Valley, *S. M. Zeller 8187* (Zeller); Sulphur Springs, *H. M. Gilkey* (Zeller 6916).

NEW ZEALAND: Canterbury, Oxford, *G. Aochir* (Cunningham 576, and Dodge); Wellington, *G. H. Cunningham*, 1928 (Dodge and Zeller); *Helen K. Dalrymple* (Lloyd Mus. 3, and Dodge).

1a. var. *MURYSPERMUS* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 373. 1935.

Type: in Zeller and Dodge Herbaria.

Fructifications globose to irregular, up to 3.5 cm. in diameter, snuff-brown to bistre, not changing on drying, surface smooth, dull, fibrils few, concolorous, not extending halfway up, not distinctly radicate, adnate-appressed; peridium thick, tough, 320–400  $\mu$  thick, of dark-brown hyphae with thin walls, somewhat vesiculose, variable in size, closely stipose; gleba with white partitions (drying yellowish) and coal-black cavities, gelatinous, cavities up to 3 mm. thick, filled with spores at maturity; septa variable in thickness, hyaline, of small hyphae up to 2.5  $\mu$  in diameter; basidia with long slender (2.5  $\mu$ ) pedicels of odd lengths, tips pyriform, 5  $\times$  7  $\mu$ , 4-spored, sterigmata short, up to 3  $\mu$  long; spores ellipsoid to citriform, black, 10–11  $\times$  7.5–9  $\mu$  (usual mature spore 11  $\times$  8.5  $\mu$ ); odor of Rhenish wine.

In strawberry patch. Oregon and California. March to April.

There were 37 fruiting bodies in the type collection. The odor is distinctive. The variety may be distinguished from the

typical species by the large cavities, white septa, the color of peridium, and more abundant spores.

OREGON: Polk County, Rickreall, *Etta Neiderheiser*, type (Zeller 2660, and Dodge); Benton County, Corvallis, *L. M. Booser* (Zeller 2346), *S. M. Zeller* 7059 (Zeller).

CALIFORNIA: Santa Clara County, Call of the Wild, *H. E. Parks* 137 (Univ. Cal. and Dodge).

2. *MELANOGASTER MACROSPORUS* Velenovsky, České Houby, 808. 1922.

Type: location unknown to us.

Fructifications tuberiform, fleshy, size of a walnut or even larger, brown when young, becoming dark horsechestnut-brown, soft, elastic, surface dull, thickly covered with long black fibrils; peridium very thin, black, not separable; gleba of black cavities with either yellowish or whitish septa, when ripe becoming gelatinous, blackish with yellowish veins; spores obovate-ellipsoid, narrower at the base, attached with 3-4 small bodies, reddish-brown, smooth, 15-18  $\mu$  long; odor very fetid.

In leaf humus of broad-leaved trees in summer, around Chuchle, common, in Trnova, Bechovice, and Karlstein. It seems to me that our fungus is *M. variegatus* Vitt. which is very often described in Germany and is quite common in other places. The spores appear ellipsoidal, 6  $\times$  10  $\mu$ ; either this size is wrong or our fungus is a new species. I have examined the spores very carefully from all points of view.—Velenovsky.

The following description is based on Oregon material which agrees closely enough with the above description to refer it here temporarily, pending opportunity to study the type:

Fructifications up to 12  $\times$  8  $\times$  6 cm. (weight 270 g. when fresh), drying russet to Mars brown and black; peridium duplex, outer layer about 140  $\mu$  thick, composed of loosely woven, periclinal, dark brown, thick-walled hyphae 7  $\mu$  in diameter, about 50  $\mu$  thick, of slender, gelified hyphae continuous with the septa; gleba black, mottled by white septa which are 90  $\mu$  thick, highly gelified; basidia evanescent; spores broadly obovoid, 12-15  $\times$  8-11  $\mu$ , dark brown; odor of spoiled silage or of onions without tear-producing qualities.

In duff under conifers, especially hemlock. Oregon. September.

OREGON: Clackamas County, on trail to Paradise Park from Twin Bridges Forest Camp, *S. M. Zeller 7759, 8330* (Dodge and Zeller); Lane County, Belknap Springs, *S. M. Zeller & G. R. Hoerner* (Zeller 8241).

3. *MELANOCASTER intermedius* (Berkeley) Zeller & Dodge, comb. nov.

*Melanogaster ambiguus* var. *intermedius* Berkeley, Ann. & Mag. Nat. Hist. I. 13: 352. 1844.

Type: in Broome Herb. at Brit. Mus. and Tulasne Herb. at Paris.

Fructifications 2–4.5 cm. in diameter, subglobose to reniform, fibrils plentiful below, at a definite place of attachment, surface even to undulating, tomentulose, very dark reddish-brown when fresh, becoming blackish where bruised, drying Prout's brown to mummy-brown; peridium 125–160  $\mu$  thick, light yellow to brownish near the exterior, stupose, of hyphae with vesiculose cells, homogeneous, but loosely woven at the surface with some erect hyphae giving the tomentulose character, distinct from the tramal tissue; gleba slaty-black, slightly lined or streaked with thin septa, of hyaline (dilute yellowish) gelified hyphae, cavities filled with spores in a gel; spores dark, mostly obovoid, obtuse, smooth, very rarely somewhat fusiform, tip subacute, 11–13  $\times$  7.4–8  $\mu$ ; odor strong, offensive, suggesting asafoetida.

Under hardwoods. England and central California.

ENGLAND: Wiltshire, Spyke Park, *C. E. Broome* (Brit. Mus. and Paris).

CALIFORNIA: *H. E. Parks*, 551, 1123, 1124; Santa Clara County, Alma, *H. E. Parks* 7, 239, 2328, 105; Sanatoga, Boys' Outing Farm, *H. E. Parks* 366; Brookdale, *H. E. Parks* 2163bis; Gundaloupe Mines, *H. E. Parks* 23, 27, 235, 2349, 145, 381, 112, 416; highway to Watsonville, *H. E. Parks* 3307; Del Norte County, Crescent City, *H. E. Parks* 2862; Humboldt County, Trinidad, *H. E. Parks* 4132, 4436, 4443 (all Univ. Cal. and Dodge).

4. *MELANOCASTER TUBERIFORMIS* Corda in Sturm, Deutschl. Fl. III. 11: 1. 1831.

*Hyperrhiza tuberiformis* Rabenhorst, Deutschl. Krypt. Fl. 1: 292–293. 1844.

Illustrations: Corda in Sturm, Deutschl. Fl. III. 11: pl. 1.

Type: Portions in Berkeley Herb. at Kew and Tulasne Herb. at Paris.

Fructifications 1.5–7 cm. in diameter when fresh, drying 1–

2 cm. (in material examined), subspherical, bay or reddish-fuscos drying Rood's brown to Vandyke brown; fibrils rare, black, appressed, basal; peridium stipose, amber to darker, 100–185  $\mu$  thick; gleba black with white or slightly yellowish, inconspicuous septa, prosenchymatous, cavities very irregular; basidia evanescent, usually 8-spored; spores obovoid, sometimes pyriform, very dark brown, smooth, 10–11.5  $\times$  5.5–7  $\mu$ .

Under *Pinus*, *Erica*, *Quercus*. Central Europe and western North America. June to August.

CZECHOSLOVAKIA: near Praha, *Corda*, type (Kew and Paris); Bohmerwald, *E. Soehner* 774 (Soehner and Dodge).

GERMANY: Spiegelslust, *E. Hesse* (Farlow).

FRANCE: Alsace, Ballon, *L. Quélet* (Upsala).

IDAHO: Priest Lake, *C. V. Piper* (Lloyd Mus. 6164).

OREGON: Benton County, Corvallis, *S. M. Zeller* 7760 (Zeller).

CALIFORNIA: no locality nor collector (Univ. Cal. 552, and Dodge); Santa Clara County, Saratoga, *H. E. Parks* 968 (Univ. Cal. and Dodge); Marin County, Mill Valley, *H. W. Harkness* 5 (Stanford).

5. *MELANOGASTER MICROSPORUS* Velenovsky, České Houby, 809. 1922.

Type: location unknown to us.

In some respects similar to *M. rubescens* but it is larger, up to 8 cm. in diameter, without odor or with weak odor of meat. Spores very small, ellipsoidal, pointed on both ends, 4–5  $\mu$ , very thick-walled, light yellow.

In leaf mould in woods in Tuchomeric. July, 1918, *J. Lissal*.—Velenovsky.

Mattirolo, Beitr. Krypt.-Fl. Schweiz (Contr. Fl. Critt. Sviss.) 8<sup>2</sup>: 37–39. 1935, described a fungus as *M. microsporus* without reference to the previous use of the name by Velenovsky. His description follows:

Fructifications irregularly globose, size of a hazel nut, yellow-umber; peridium 150  $\mu$  thick, of three layers, the outer forming a tomentum, the middle deeply colored, of slender crowded hyphae, the inner layer hyaline, thicker, pseudoparenchymatous; gleba chestnut to fuliginous; basidia clavate, 4-spored; spores ellipsoidal, 3–4  $\times$  2  $\mu$ , similar to those of *Rhizogon rubescens*.

Under chestnut and pine. Rodero. Como Province.

6. *MELANOGASTER BROOMEIANUS* Berkeley in Tulasne, Ann. Sci. Nat. Bot. II. 19: 377. 1843; Ann. & Mag. Nat. Hist. I. 13: 353. 1844.

*Melanogaster variegatus* var. *Broomeianus* Tulasne, Fung. Hypog. 93. 1851.

*Tuber moschatum* Sowerby, English Fung. pl. 426. 1815.—*non al.*

Illustrations: Tulasne, Ann. Sci. Nat. Bot. II. 19: pl. 18, f. 23.

Fructifications subglobose to irregularly lobed, often coalescing when cespitose, 2–4 cm. in diameter; surface ochraceous then Dresden brown with a flesh tint, becoming blackish where handled, drying tawny-olive to warm sepia, appressedly tomentulose; brownish fibrils below; peridium variable in thickness, 50–200  $\mu$  thick (mostly 50–100  $\mu$ ), of stupose prosenchyma with large vesiculose cells, yellow-amber to darker toward the exterior, extending as fundamental tissue into the trama; gleba sooty-black, gelified, tramal septiments white to creamy, of subgelatinous hyaline hyphae, cavities filled with spores in a gel; spores light brown, narrowly oblong, broadly truncate below, (5–) 6–8.4 (–11)  $\times$  (2.5–) 3.5–4.0 (–4.5)  $\mu$ ; odor of coffee grounds.

Under hardwood trees. July to February. Europe, Michigan, Indiana, and Oregon.

Close to *M. rubescens* in spore characters, but the spores are darker and definitely truncate below. Peanut-shaped spores are seldom found in this species, but even so they retain the truncate character.

EXSICCATI: Berkeley, British Fungi, 285.

U. S. S. R. [Kurland]: Lesten, *F. Bucholtz* (Farlow); Kuruka, Ternomorek, *F. Bucholtz* (Farlow); Moskva, Ocfaltshebe, *F. Bucholtz* (Farlow); Mikhailovskoe, *Bucholtz*, Aug. 4, 1899 (Farlow); Ucrania, *Csernasev* (Upsala).

SWEDEN: Upland, Upsala, Karolinaparken, *E. P. Fries*, 1853 (Upsala); *Th. M. Fries*, 1877, 1883 (Upsala); *Seth Lundell*, 1930 (Upsala and Dodge); *Harry Smith*, 1930 (Upsala and Dodge); Valby, Lidehall, *C. J. Cederstrom*, 18–10–91 (Upsala); Skåne, Ramlösa, *E. Melin* (Upsala).

AUSTRIA: Tirol, Füssen, *J. R. Weir* 22,291 (Dodge).

GERMANY: Würzburg, *E. Soehner* 1033 (Soehner and Dodge).

SWITZERLAND: Neuchatel, *P. Konrad* (Lloyd Mus. 050, and Dodge); Genève, Miolan, *J. Muller* (Lloyd Mus. 05915, Dodge, and Stanford, ex herb. G. Winter).



ITALY: Como, Rodero, *O. Mattiolo*, Aug. and Oct. 1900 (Lloyd Mus. 081, 03709, Dodge); near Milano, *no collector* (Stanford, ex herb. G. Winter); Trentino, *G. Bresadola* (Upsala).

FRANCE: Alsace, *L. Quélet* (Paris); Eure, Andelys, *G. Malençon* (Dodge); Loiret, Port pres Gien, *L. Tulasne*, Oct. 1843 (Paris); Seine-et-Marne, Vincennes, *L. Tulasne* (Paris); Versailles, *L. Tulasne* (Paris).

ENGLAND: Wiltshire, Rudloe, *C. E. Broome*, Oct. 11, 1842 (Brit. Mus., and Brown Univ.); without locality, *Berkeley*, British Fungi, 285.

MICHIGAN: Ann Arbor, *L. E. Ekvall* 19 (Univ. Mich.); Saginaw Forest, *C. H. Kauffman* 22 (Univ. Mich.); School Girls Glen, *A. H. Smith* (Univ. Mich.).

INDIANA: Lafayette, Happy Hollow, *H. S. Jackson* (Dodge, and Zeller 2806).

OREGON: Benton County, Corvallis, *S. M. Zeller* 1787, 1898, 3242 (Zeller); Wren, *L. M. Booser* (Zeller 855); Lincoln County, Waldport, *S. M. Zeller* 4996 (Zeller).

# 7. *MELANOGASTER RUBESCENS* (Vittadini) Tulasne, Fung. Hypog. 96. 1851.

*Octaviania rubescens* Vittadini, Monogr. Tuberac. 18. 1831.

*Hyperrhiza rubescens* Rabenhorst, Deutschl. Krypt.-Fl. 1: 293. 1844.

*Bondatia oleodora* Lespiault, herb. nom.

*Melanogaster nauseosus* Coker & Couch, Gast. Eastern U. S. & Canada, 39. 1928.

Type: in Broome Herb. at Brit. Mus., Berkeley Herb. at Kew, and Tulasne Herb. at Paris. The type of *M. nauseosus* from Univ. North Carolina Herb.

Fructifications subglobose to elongate, irregularly sulcate, 1.5–3 cm. in diameter; surface tomentulose, even to reticulately ridged, light brownish when fresh, drying raw umber or darker; fibrils absent; peridium spongy, stupose, homogeneous, darker brown toward outer surface, drying 100–200  $\mu$  thick, distinct from tramal tissues; gleba moist, bluish-white when fresh, reddening and yellowing when freshly cut, drying brownish-black; septa broad, variable, cinnamon-buff; cavities rounded, not crowded, at first filled with dark claret-brown or darker spore masses, later becoming hollow, due to the relatively few spores scattered through the cavity gel; basidia clavate, unevenly distributed on the branching hyphae of the cavities; spores oblong-fusiform to ovoid-ellipsoid, or curved, somewhat irregular (often the shape of the fruit of *Arachis hypogaea*), 8–9.6 (–11.8)  $\times$  5.5–6.5  $\mu$ , light yellow, pollucid.

Southwestern Europe and eastern North America. July to November.

The specimen from Italy collected by Mattiolo differs from the other material of this species in having long narrow spores which measure  $11-13 \times 3.5-4 \mu$ . It is with some hesitation that we have referred this specimen to *M. rubescens* (Vitt.) Tul.

The specimen from Ithaca, in alcohol, shows a peridium 650–750  $\mu$  thick, drying as thin as the peridium in the type.

ITALY: Como, Rodero, *O. Mattiolo*, Oct. 1905 (Dodge); Lombardia, near Milano, *C. Vittadini*, type (Paris, Kew, and Brit. Mus.).

FRANCE: Lot-et-Garonne, Nérac, *Lespiault* (*Bondatia oleodora* herb nom., Paris).

NEW YORK: Ithaca, Beebe Lake, *H. H. Whetzel* (Atkinson Herb. at Cornell 13679, Dodge, and Zeller 1446).

PENNSYLVANIA: Mt. Pocono, *Schweinits* 2210 (sub *Rhizopogon aestivus* in Curtis Herb. at Farlow).

NORTH CAROLINA: Orange County, Chapel Hill, *J. N. & E. E. Couch* (type of *M. nauseosus*, Univ. N. C. 8281); Watauga County, Blowing Rock, *Coker et al.* (Univ. N. C. 5804).

ALABAMA: Scpsly, Payne's Mills, *P. P. Payne* (Lloyd Mus. 041).

#### 8. *MELANOGASTER Parksii* Zeller & Dodge, sp. nov.

Type: Univ. Cal., Dodge, and Zeller Herbaria.

Fructificationes irregulares vel subsphaericae, 2–4 cm. diametro, fibrillae basi prominentes, brunneae nigrescentes, siccatae “Dresden brown” vel “Mars brown,” obscuriores contusae, superficie aequo vel undulato, tomentuloso vel glabro; peridium prosenchymaticum, cellulis magnis spongiosis contextum, dilute luteum, externe obscurius, 300–480  $\mu$  crassitudine; gleba “Brussels brown” vel “warm buff” siccata, locellis in centro fructificationis subcavis; basidia non visa; sporae late obovoideae vel subsphaeroideae, dilute brunneae, sub lente pellucidae,  $8-9.6 \times 6.7-7.7 \mu$ .

Fructifications irregular to subspherical, 2–4 cm. in diameter, dark brown to black, drying Dresden brown to Mars brown, darker where bruised, surface even or undulating, tomentulose to glabrous, basal fibrils prominent; peridium spongy, prosenchymatous, of large cells, light yellow, darker toward the peridium, 300–480  $\mu$  thick; gleba Brussels brown [dry], central cavities more or less hollow when dry with whitish or warm buff, gelified septa; basidia not seen; spores broadly obovoid to subspheroid, light brown, pellucid,  $8-9.6 \times 6.7-7.7 \mu$ ; odor pungent, spreading.

Deeply buried under leaves of *Quercus agrifolia*. California. April.

CALIFORNIA: Santa Clara County, Call of the Wild, *H. E. Parks 136a* (Univ. Cal., Dodge, and Zeller 1412); Guadalupe Mines, *H. E. Parks 136*, type (Univ. Cal., Dodge, and Zeller 1655).

9. *MELANOGASTER MOLLIS* Lloyd, Myc. Notes 65: 1047. 1921 (see also p. 1065).

Illustrations: Lloyd, Myc. Notes 65: *f. 1939*.

Type: In Lloyd Mus., Dodge, and Zeller Herbaria.

Fructifications subglobose, collapsing at maturity, 2.5–3 cm. in diameter, drying Dresden brown to mummy-brown, pruinose to smooth where rubbed, distinct fibrils below; peridium thin, 80–130  $\mu$  thick, simplex, stipose, hyaline with brownish exterior; gleba in general black, drying hollow, tramal tissues whitish, then gelatinizing, prosenchymatous, basidia-bearing cavities filled with the deliquescent hyphae, basidia, and spores; spores small, dark brown, ellipsoid, smooth, 5.5–6.7  $\times$  2–3.7  $\mu$ ; odor disagreeable, rancid.

In black vegetable humus, hypogeous or emersed, among greasewood.

*Melanogaster mollis* Lloyd (except for *M. microsporus*) has the smallest spores of any known species. In the type collection the fructifications are extremely mature, with the gleba becoming deliquescent, drying with large hollows.

WYOMING: [Fremont County, Meeteetse, 6700 feet alt.], *Simon Davis*,<sup>1</sup> type (Lloyd Mus. 041, Dodge, and Zeller).

PORTUGAL: *J. Rick* (Lloyd Mus. 05348, and Dodge).

10. *MELANOGASTER DURISSIMUS* Cooke, Grevillea 7: 94. 1879.

Type: India, Chakrata, 8000' north of Delhi, *Baden Powell*.

Fructifications compressed, sulcate, subspherical to reniform, smooth, up to 4 cm. in diameter, drying 2  $\times$  1  $\times$  1 cm., very hard, dark fuscous to sepia, cottony-furfuraceous, rubbing glabrous, no fibrils; peridium stipose, 90–115  $\mu$  thick, amber; gleba black with buff-white septa of close gelified pros-

<sup>1</sup> Lloyd did not record the data on this specimen, and the late Mrs. E. B. Blackford assured Dodge that she has been unable to locate a duplicate in Simon Davis' collections but she found notes for *Calvatia defodioides* Lloyd from this locality, and it is probable that all of his collections from Wyoming came from the same locality.

enchyma; basidia evanescent; spores  $6-8 \times 4-5 \mu$ , ellipsoid, very truncate at base, smooth, dark brown, exospore not conspicuous.

British India. November to February.

Baden Powell, the collector of the type, notes that this species is cooked and eaten by the natives, who report that chewing a little piece keeps off thirst in crossing high passes. The natives report it common in the hills of Kangra and in the Upper Chenab valley.

BRITISH INDIA: Chakrata, *B. Powell*, type (?); Simla, *J. M. Clark*, 7 Feb. 1879 (Brit. Mus. and Kew); *J. H. Burhill*, Nov. 8, 1902 (Lloyd Mus. 7331, com. E. J. Butler 14945).

11. *MELANOASTER VARIEGATUS* (Vittadini) Tulasne, Ann. Sci. Nat. Bot. II. 19: 377. 1843.

*Octaviania variegata* Vittadini, Monogr. Tuberac. 16. 1831.

?*Tuber moschatum* Bull. Champ. 1: 79. 1789.

*Hyperrhiza variegata* Rabenhorst, Deutschl. Krypt.-Fl. 1: 293. 1844.—*non al.*

Illustrations: Vittadini, Monogr. Tuberac. *pl.* 3, *f.* 4; Bull. Champ. 1: *pl.* 479.

Type: della Pistola and along R. Lambro near Milano, Lombardia, *Vittadini*. Specimens sent by Vittadini in Sprague Collection at Harvard Univ., in Berkeley Herb. at Kew, and in Paris (com. Ardissonne).

Fructifications rounded, irregular, the size of a hen's egg or fist, drying 2 cm. in greatest diameter, smooth, ochraceo-ferugineous drying Verona brown, fibrils basal, fuscous; peridium stipose,  $100-160 \mu$  thick, amber-yellowish, extending as fundamental tissue into the trama; gleba yellowish-ashy at first, becoming black, with thin yellow-orange septa, cavities subpentagonal; basidia evanescent; spores ellipsoidal, very dark brown,  $7.5-10 \times 5-7.5 \mu$ , smooth.

Under *Quercus* and *Cistus monspeliensis*. Northern Italy, Algeria, and California. August to December.

It is with some hesitation that we have referred *Parks Z22* to this species, owing to its texture resembling *Hymenogaster*, and to the absence of gel filling the cavities.

ITALY: Lombardia, *C. Vittadini*, type (Paris, com. Ardissonne, Kew, and Farlow); agro panormilano, *Insenga* (det. *Tuber Borchii*, Paris).

ALGERIA: Alger, *Durieu de Maisonneuve* (Paris).

CALIFORNIA: Santa Clara County, Guadalupe Mines, *H. E. Parks 958* (Univ. Cal. and Dodge); Saratoga, *H. E. Parks 292* (Univ. Cal., Dodge, and Zeller); Marin County, San Rafael, *H. E. Parks 2059* (Univ. Cal.).

#### DOUBTFUL SPECIES

MELANOASTER SARCOMELAS (*Vittadini*) Tulasne, Fung. Hypog. 97. 1851.

*Octaviania sarcomelas* Vittadini, Monogr. Tuberac. 16. 1831.

*Hyperrhiza sarcomelas* Rabenhorst, Deutschl. Krypt.-Fl. 1: 293. 1944.

Type: Lombardia, *Vittadini*, not seen.

Fructifications small, irregular; peridium smooth, without rooting appendages; gleba very black, uniform in color; cells regular, contents gelified, filled with spores; spores ovoid, smooth, somewhat larger. Strong odor of ink. Fungus the size and form of a seed of *Faba*, with a thin peridium; base hardly distinguishable. Cavities rhomboidal or pentagonal, septa ashy, pellucid, opaque in center. When dry contracting into a solid perennial mass.—Vittadini.

A careful study of the original descriptions of Vittadini's species suggests that *M. sarcomelas* may be a synonym of *M. tuberiformis* Corda. In spite of searches by Tulasne, Mattiolo, and Lloyd, the type of this species has not been found.

MELANOASTER ODORATISSIMUS (Vitt.) Tulasne, Fung. Hypog. 95-96. 1851.

*Octaviania odoratissima* Vittadini, Monogr. Tuberac. 19. 1831.

*Hyperrhiza odoratissima* Rabenhorst, Deutschl. Krypt.-Fl. 1: 293. 1844.

Type: two fructifications from oak woods across the Po near Milano, *Vittadini*, April, probably lost.

Fructifications subspherical, sub-smooth, golden-rufous, with basal appendage. Gleba tough, pulpy, rufous-brown with septa; cavities not conspicuous, never empty; spores ovoid, umber. Odor of *Hya-cinthus botryoides*. Fructifications the size of a chestnut; peridium with rooting fibrils as in *M. variegatus*, golden at first, then rufous;

gleba suggesting the pulp of red beets; cavities not very distinct; spores rare.—Vittadini.

Hesse, 'Die Hypogaeen Deutschlands' 1: 64-65, *pl. 4, f. 10-14, pl. 8, f. 8*. 1891, has referred here material collected at Michelbach near Marburg, in 1884, but we have been unable to see this material. He describes it as follows:

Fructifications spherical, from size of a large hazel-nut to that of a sparrow egg, golden-yellow becoming deep red-brown, smooth, odor of *Hyacinthus botryoides*; peridium not easily separable from the gleba, composed of gelified hyphae, becoming deep reddish-brown; septa at first golden, becoming reddish; clamp connections prominent in the mycelium of the cavities bearing the basidia, which are mostly 8-spored; spores almost ovoid [figures show them ellipsoid to almost allantoid], brown, size not given, but if magnification of figures is correct spores about  $7-8 \times 4-5 \mu$ .

There seems little to distinguish Hesse's concept of *M. odoratissimus* from *M. Broomeianus* Berk.

*BULLARDIA INQUINANS* Junghuhn, Linnaea 5: 408. 1830.

*Argyrium inquinans* Wallroth, Fl. Cryptog. Germ. 2: 873. 1833.

*Hyperrhiza inquinans* Rabenhorst, Deutschl. Krypt.-Fl. 1: 292. 1844.

Illustrations: Junghuhn, Linnaea 5: *pl. 6, f. 15*.

Type: Germany: between Rammelburg and Klaus, *F. Junghuhn*, not seen.

Fructifications up to the size of a walnut, irregular, gibbous, smooth; peridium thin, sometimes ruptured at maturity; fibrils sparse, appressed; gleba black; septa white, composed of branched, loosely woven hyphae; basidia scattered throughout the cavities; spores black. Odor sweet, pleasant, almost aromatic; taste very sweet.—Junghuhn.

Under *Corylus Avellana* L. Germany. September.

While there seems no doubt that the above description refers to a species of *Melanogaster*, it is too brief and generalized to refer definitely to a species. It is probably not *M. variegatus*, to which it has been generally referred, as that Mediterranean

species is not known north of the Alps. It is much more probably *M. tuberiformis* or *M. Broomeianus*.

MELANOGASTER TUBEROSUM (Fr.)

*Polysaccum tuberosum* Fries, Syst. Myc. 3: 55. 1829; Linnaea 5: 695. 1830.

*Lycoperdoides tuberosum*, ferrugineum, arrhizon, pulpa nigra, Micheli, Nova Pl. Gen. 219. 1729.

*Hyperrhiza tuberosa* Fries, Ind. Syst. Myc. 102. 1832; Summa Veg. Scand. 437. 1849.

cf. Th. M. Fries, Svensk Bot. Tidskr. 3: 293. 1909.

Illustrations: Micheli, Nova Gen. Pl. pl. 98, f. 2.

Type: "In pratis calcareis," Malmö, Sweden, along with *Bovista suberosa*. Angelin:

Fructifications without roots, round, irregular, often oblong, suggesting a small tuber of *Solanum*, the size of a walnut (*Juglans*), soft when young, becoming hard; peridium coriaceous, ferrugineous, smooth, almost pruinose under a lens, not dehiscent; gleba with white or yellow septa, cavities very black, large, round or irregular, producing a black viscid ink with a very foul odor, filled with spores when mature; no capillitium.—Fries.

Since *M. Broomeanus* Berk. is the only species of this genus so far found in Sweden, of which we have seen specimens, it is likely that *M. tuberosum* may be the same fungus. However, we prefer not to reduce *M. Broomeanus* to synonymy until we have had an opportunity to study the type, if it still survives.

MELANOGASTER AUREUS (Vittadini) Tulasne, Fung. Hypog. 97. 1851.

*Octaviania aurea* Vittadini, Monogr. Tuberac. 20. 1831.

*Hyperrhiza aurea* Rabenhorst, Deutschl. Krypt.-Fl. 1: 293. 1844.

Illustrations: Vittadini, Monogr. Tuberac. pl. 3, f. 14.

Type: in forest on hill near La Stradella, near Milano, summer, C. Vittadini, apparently lost.

Fructification oblong, reniform, rooting at the base, peridium smooth, at first whitish. Gleba hard at first, golden, with white veins (septa) variegated, then soft, blackening, somewhat hollow.

Odor pleasant. Fungus size of a filbert, peridium thin, becoming fuscous at the touch, with a radiceiform appendage. Cavities not numerous, rounded or elongate, suggesting the pores of *Boletus*, golden-shining within. Septa thick, whitish-citrine. Cut gleba becoming greenish, but at maturity breaking down into a blackish sporiferous pulp.—Vittadini.

#### EXCLUDED SPECIES

*Melanogaster Wilsonii* Lloyd, Myc. Notes 68: 1176, 1923, is RHIZOPOGON **Wilsonii**. Zeller & Dodge, comb. nov.

*Melanogaster carolinensis* (Bosc) DeToni in Sacc. Syll. Fung. 7: 167. 1888.

*Uperhiza* Bosc, Ges. Naturf. Freunde Berlin Mag. 5: 88, pl. 6, f. 62. 1811.

*Uperhiza carolinensis* Nees ab Esenbeck, Syst. d. Pilze 1: 159. pl. 15, f. 146. 1816.

*Hyperhiza caroliniensis* Sprengel, Syst. Veg. 4: 416. 1827.

*Uperhiza Boscii* Schweinitz, Syn. Am. Bor. 255. 1834; Lloyd, Myc. Notes 30: 395. 1908. Curtis states that the Schweinitz specimen is a bad *Scleroderma*? from Mt. Pocono, Pa.

Type: Carolina, Bosc; probably lost.

A careful study of the original description and figures suggests *Scleroderma* sp. but in the absence of the type its identity remains doubtful.





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New scientific names of plants and the final members of new combinations are printed in **bold face** type; synonyms and page numbers having reference to figures and plates, in *italics*; and previously published names and all other matter, in ordinary type.

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